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# REACTIONS OF THE HONEYBEE TO LIGHT

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# REACTIONS OF THE HONEYBEE TO LIGHT[1]

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## I. EXTENT OF THE SPECTRUM FOR THE HONEYBEE AND THE DISTRIBUTION OF ITS STIMULATIVE EFFICIENCY

### INTRODUCTION

In considering the reactions of a given animal to light of different wave lengths there are three fundamental questions which perhaps come first to mind: (1) The extent of the spectrum for this animal—that is, the wave lengths of the shortest and longest radiations to which it responds, (2) the relative efficiency of the different wave lengths in eliciting the same response, and (3) the extent to which the animal distinguishes the different wave lengths, or the number of chromas that it distinguishes.

The last of these questions is discussed in Part II of this paper, but the first two may properly be considered now. Before asking these questions in regard to the honeybee in particular, however, it may be well, for comparison, to review briefly our knowledge of the spectra for other animals, so far as investigation has revealed. The results of the more important investigations follow: The spectrum for man (*12*) [3] is said to extend from about wave length 400 mμ at the violet end to about 770 mμ at the red end,[4] the chicken from 500 to 700 (*19*), the pigeon from 424 to 704 (*26*), the alligator from 398 to 704 (*26*), the fish Phoxinus from about 340 to about 800 (*37*), the blowfly larva from about 422 to 625 (*30*), the water flea Daphnia as low as 228 (*3*), the cyprid larva of the barnacle Balanus from 355 to 690 (*36*), the clam *Mya arenaria* from about 420 to about 650 (*14*), the larva of the worm Arenicola from 442 to 534 (*30*), the earthworm from 463 to 514 (*30*), Cerianthus from 460 to about 653 (*31*), Volvox from 434 to 655 (*27*), and in an investigation of 12 protozoa (*30*) the spectrum

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[1] Received for publication Oct. 27, 1930; issued April, 1931. Parts I and II of this paper were presented as a dissertation in partial fulfillment of the requirements for the degree of doctor of philosophy, received in June, 1928, from the Johns Hopkins University, where the writer was a Bruce Fellow. The work upon which they were based, as well as that of Part III, was done while the writer was in the status, first, of junior biologist in apiculture and, later, of field assistant, division of bee culture, Bureau of Entomology, U. S. Department of Agriculture. The experimental work of the first two parts was done largely in the laboratory of the division of bee culture, and in part at the zoological laboratory of the Johns Hopkins University. That of Part III, and the final preparation of the manuscript, were done at the bee culture laboratory.

[2] Now professor of biology, Western Maryland College, Westminster, Md. The writer is indebted to S. O. Mast, of the Johns Hopkins University, for suggesting the problems here considered and giving general supervision to the work on Parts I and II; to James I. Hambleton, in charge of the division of bee culture, Bureau of Entomology, for making possible the investigations and furnishing laboratory facilities; to A. L. Colton, of the Bureau of Entomology, for helpful suggestions on statistical and mathematical questions; to W. W. Coblentz, of the Bureau of Standards, U. S. Department of Commerce, for determinations of spectral energy; and to all here named for much kindly advice.

[3] Reference is made by number (italic) to Literature Cited, p. 417.

[4] A high limit of 850 has been reported (*34, p. 103*) and a low limit of 210 (*29*). The writer can see ultraviolet as low as wave length 365 mμ when his eyes are fully adapted to darkness.

was found to extend from between 422 and 483 at the violet end to between 504 and 646 at the red end.

A word of caution against taking these and similar data too literally is perhaps advisable here. It must be remembered that the difficulties involved in such studies as those cited are very great. In the first place, it is difficult to compare man with other animals, since with man the subject can speak of his subjective impressions, but with other animals one has to observe some physical response as a proof that the light is having an effect. If the light has an effect which is subminimal to the response which one is observing there is no way of ascertaining that fact. In the second place, owing to the difficulty of controlling accurately the wave length of the light used, it is not easy to determine exactly the limits of the spectrum for an animal. The various light filters often employed, although transmitting much of the incident light, transmit at the same time a wide band of wave lengths, with different proportions of each. On the other hand, the sections of a pure prismatic spectrum such as is sometimes employed, although much more homogeneous in wave length, are often too weak to elicit a response at a particular wave length. In the third place, it is often true that an animal still responds at the shortest or even the longest wave length producible by the apparatus used. In such an instance one obviously can not be sure whether he has reached the animal's limit of vision. And even in case the limit has been reached at a given intensity of illumination, there is no reason to suppose that this is an absolute limit, and would not extend farther if the intensity were increased.

Notwithstanding these and other considerations which make it impossible to state precisely and unconditionally what the extent of the spectrum is for a particular animal, certain conclusions may be drawn. It is apparent that the average human eye under usual conditions is sensitive to radiations ranging in wave length between about 400 and 770 m$\mu$. The range for man extends on the red end of the spectrum farther than the range for most of the other animals. Several of the experimenters remark on the fact that red light to which they themselves are sensitive does not seem to stimulate the animals in question. However, in birds, and possibly also in fishes, the opposite seems to hold. Honigmann (*19*) says that for chickens the region around wave length 660 m$\mu$ is four times as stimulative as for man, and the fish *Phoxinus laevis* has been credited with being sensitive to radiations of wave lengths nearly or quite as long as 800 m$\mu$ (*37*). On the other hand, it is fairly common to find animals sensitive to the shorter wave lengths in the deep blue and violet, e. g., at 425 m$\mu$. Some are said to exceed man in this respect, the fish just mentioned being sensitive to radiations at 340 m$\mu$ and Daphnia even to those at 228 m$\mu$.

But what of the honeybee in particular? There has been no direct research on this problem with honeybees, but there is considerable evidence to be derived from the so-called training experiments of Von Frisch (*7*) and Kühn (*22*). These men first trained the bees to associate a given color with food, and then observed whether or not the bees confused that color with other colors or with various shades of gray. Von Frisch, for example, found that after training bees to come for food placed exclusively on red paper, and then after shifting the position of the red in relation to that of various gray papers presented at

the same time, the bees confused dark gray and black with red, although they did not confuse yellow, or blue, or violet, with any gray. This result indicates that the paper which appears red to us appears very dark, almost black, to bees; in other words, that their spectrum does not extend as far into the red as our own.

Kühn (*22*), using spectral colors instead of colored papers, got results essentially similar to those of Von Frisch in regard to red. More precisely, he maintains that the bee does not respond to wave lengths longer than 650 mμ. In addition, however, he found that his bees were stimulated by regions of the ultra-violet as low as that of wave length 313 mμ, ordinarily invisible to man. And not only were they stimulated, but after being trained to associate the wave lengths 313 mμ and 365 mμ with the presence of food, they did not confuse these two regions with any other region of the spectrum which he tried—a result which indicates that they see this ultra-violet light as a color distinct from all colors visible to us, and not merely as a fluorescence, and that, consequently, the spectrum visible to them extends at least as far into the ultra-violet as the wave length 313 mμ.

In regard to the honeybee, nothing at all has been known as to what region of the spectrum is most efficient in stimulating it. If it is true that the spectrum visible to the bee extends from wave length 313 mμ in the ultra-violet up to 650 mμ in the orange-red, we should expect to find the maximum point, judging from the usual results, somewhere more than halfway toward the ultra-violet end of the spectrum, probably in the blue. Or perhaps there are two maxima, one in the usual green or greenish-yellow region and another in the violet or ultra-violet. To determine the relative stimulative efficiency of the various parts of the spectrum to which the bee reacts, and to ascertain more carefully its limits, thus become especially alluring problems. The experiments to be described were designed to throw some light on them.

In regard to the second question mentioned at the beginning of this introduction—namely, the relative stimulative efficiency of different wave lengths—comparatively little is known except with respect to the human eye. For man a summary of the various investigations (*12*) places the point of maximum efficiency between the wave lengths 550 and 560 mμ. This standard curve is reproduced in Figure 4 (dotted curve). For other animals the most reliable investigations give the following results: For the chicken (*19, p. 68*) the maximum efficiency is between 560 and 580 mμ, for the pigeon (*26*) it is at 564, for the alligator (*26*) it is at 544, for the fish Phoxinus (*37*) it is probably at 592,[5] for the blowfly larva (*30*) at 504, for the cyprid larva of Balanus (*36*) at about 540, for *Mya arenaria* (*14*) at about 500, for the Arenicola larva and the earthworm (*30*) at 483, for Cerianthus (*31*) at about 532, for Volvox (*27*) at about 494, and for various protozoa (*30*) it ranges between 534 and 473, the location depending on the animal. Taken as a whole, the region of the spectrum most efficient in stimulating animals, so far as these data show, is somewhere between the blue-green and the yellow region; in other words, somewhere between the wave lengths 473 and 580 mμ, according to the particular animal. Only in birds and possibly in fishes does the maximum lie farther toward the red end of the spectrum than in man; in all others it lies

[5] This is the region which the fish most readily learns to associate with food; it may not be the region of actual maximum efficiency.

farther toward the violet end. Where complete curves of the distribution of stimulative efficiency in the spectrum have been worked out they are similar to the curve for man presented in Figure 4. In the curve for any given animal the maximum is nearly always not exactly in the center of the curve, but lies slightly skewed toward the violet end.

## METHODS AND RESULTS

One of the most successful methods of finding the relative stimulative efficiency of various wave lengths which are unequal in energy is the one used by Mast in 1917 (*30*). The procedure is, briefly, as follows: The animals are exposed simultaneously to a spectral color and to white light of a measurably variable intensity. This intensity is then varied until the animals react equally to both beams. Then another spectral color is chosen and again the white is equated to it, and so on for as many as may be desired, or as is possible with the apparatus at hand. The relative intensities of the white then represent the relative stimulation caused by the various spectral colors. It should be emphasized that the white is adjusted until its effect on the animal is *equal* to that of each spectral color used; this is a point that will be referred to later. Having found the relative *effect* of each spectral color, the relative *efficiency* of each can then be calculated by simply dividing the relative effect by the relative energy transmitted at that wave length.

This method, in essentials, was used in the experiments here described, although several modifications had to be made, which will be considered at the proper place.

At the bee culture laboratory there was available a spectroscope of the constant-deviation type, with which to obtain light of the wave lengths desired. A 400-watt gas-filled projection lamp having a tungsten filament furnished the light for the spectrum. The width of the collimator slit of the spectroscope was made 1.8 mm. and that of the telescope slit 1.05 mm. The graduated head of the instrument, directly denoting the wave length of the light used, read from 430 mμ to 700 mμ. The readings for these experiments were chosen at intervals of 20 mμ from 430 mμ, giving 13 steps up to and including 690 mμ, or, in all, 14 wave lengths. On subsequent calibration of the instrument with a helium tube, the indicated wave length 430 mμ was found to be really 431 mμ, and 690 mμ to be really 697.5 mμ, with intermediate points proportionately in error; the corrected values are therefore substituted for those indicated by the instrument. It is recognized, of course, that a slit 1.05 mm in width will not give monochromatic light. The length of spectrum able to pass a telescope slit of given width is, in a prismatic spectrum, greater for the longer waves than for the shorter waves, owing to the greater refraction of the latter. Thus, in this apparatus the light said to have a wave length of 431 mμ was in reality the aggregate of a band extending approximately from 429 mμ to 433 mμ, and similarly that called 690 mμ was a band extending approximately from 675 mμ to 705 mμ, those between varying proportionately.

The first problem was the arrangement of an apparatus in which the bees would react primarily to light and not to other stimuli. For example, one of the most disturbing factors in such work as this is the tendency of bees in close confinement simply to race continuously around the sides of the container, apparently in a frantic effort to escape, and to disregard the light almost entirely. It was

found that to remedy this difficulty the container must be made so large that even with its great activity the bee will seldom strike the sides, but will be able to roam in comparative freedom over a large space. Every effort to confine the bee to narrow paths or make it go through small openings resulted in almost complete substitution of contact reactions for light reactions. After a number of tests the need was satisfactorily met. A shallow, rectangular box, 65 by 25 by 4 cm., was made and covered with a wire screen. Through a g ass-covered opening in the middle of one end of this box a narrow beam of light from an ordinary electric bulb could be projected, and through two openings in the opposite end, each closed with a diffusive screen of ground glass, the light from the spectroscope and white light from a comparison lamp could be projected simultaneously, the two screens being of the same shape and size. Each screen was at the end of a tunnel, the two tunnels extending across the

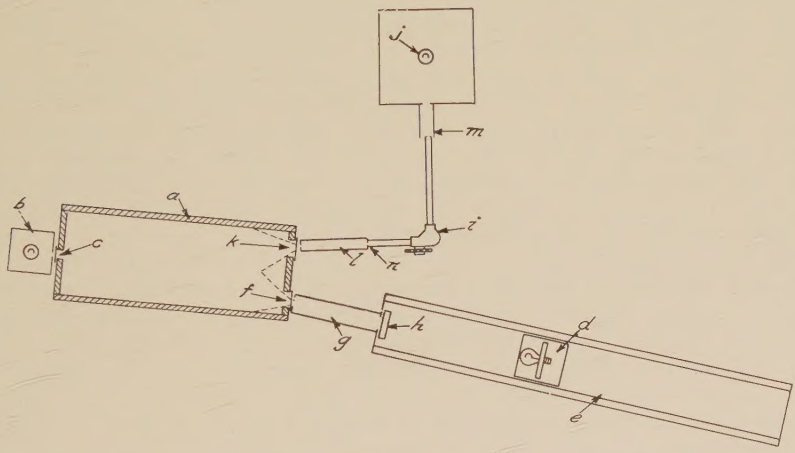


FIGURE 1.—Arrangement of apparatus used to ascertain the relative stimulative effect of spectral rays upon bees; *a*, box in which the bees were inclosed for experimentation; *b*, box containing electric bulb to illuminate ground glass at aperture *c*; *d*, comparison lamp, inclosed in box *e*, and illuminating ground glass at aperture *f*, through tube *g*; *h*, cell containing solution of cupric sulphate; *i*, spectroscope, illuminated by electric lamp *j*, and directing beam of colored light on ground glass at aperture *k* through tube *l*; *m*, collimator slit; *n*, telescope slit

width of the box. The apparatus was, of course, set up in the dark room.

The diagram, Figure 1, is inserted to convey a better idea of the arrangement of the apparatus. The box *a* is 65 by 25 by 4 cm. in size, and covered with a wire screen; in this the bees were confined; *b*, a box, 15 by 15 by 15 cm., in which was placed a 15-watt electric bulb, to illuminate a piece of ground glass which covers the aperture *c* connecting *a* and *b;* at the end of *a*, opposite this aperture, are two passages, with flaring sides, leading to the two apertures *f* and *k*, each covered with ground glass. The ground glass at *f* was illuminated by the 100-watt "comparison lamp" *d*, which was inclosed in a box, *e*, 117 cm. long and provided with guides for conveniently adjusting the distance of the lamp from the ground glass. The only light escaping from this box was emitted through an opening in one end of it, 26 cm. from the ground glass, this opening and the aperture *f* being connected by a tube *g* to prevent

diffusion of the light. At the end of this box, covering the opening, was a glass vessel, *h*, containing a dilute solution of cupric sulphate, to eliminate infra-red light. The glass of this vessel and of the diffusion screens also eliminated ultra-violet. The aperture *k* was connected by a tube *l* with the slit through which the light of the wave length chosen was emitted from the spectroscope.

As has been stated, the spectroscope *i* is of the constant-deviation type, with a graduated head for controlling the wave length of light to be emitted by the slit *n* and thrown on the ground glass at the aperture *k*. The collimator slit *m* was illuminated by a 400-watt electric lamp, *j*, inclosed to prevent the escape of light and placed at a suitable distance.

As a beginning of the routine of experimentation, 10 bees were caught at a feeder or on flowers[6] and were put into the box. A feeder, consisting of a bottle of sugar water, its mouth covered with cloth, was then inverted on the wire screen and the light of the dark room turned off. The bees soon collected on the cloth and began to feed. They were left in darkness for from three to five minutes; in this time they became satiated with sugar water, and quieter and less excitable. They also became somewhat adapted to the darkness. The small lamp (in box *b*, fig. 1) illuminating the opening at the center of one end of the box was then turned on and left until the bees congregated at this end, then turned off, and simultaneously the spectroscope lamp and the comparison lamp were turned on, each producing an illuminated area of the same size on the ground-glass screen used with it at the opposite end of the box. Most of the bees then went toward these areas, part entering one of the two flaring tunnels (fig. 1, *f* and *k*) and part the other, sometimes a few entering neither, but wandering aimlessly, without direction. After the bees entering each tunnel had been counted, the lamp at the opposite end was again turned on and the opening there illuminated until the bees congregated at that end (fig. 1, *c*), then the whole process was repeated. The 10 bees were thus induced to react over and over again until they began to appear sluggish and somewhat indifferent to the light. Ordinarily about 150 positive reactions were obtained from 10 bees. As soon as the bees became unfit for further use they were removed from the box, taken into the open, and released. Then 10 more field bees were captured and put into the box, and 150 positive reactions again obtained, and this procedure was continued as long as desired.

In the earlier experiments an attempt was made so to adjust, by changing the distance of the lamp, the intensity of the beam of white light that the response induced by it equaled that induced by the beam from the spectroscope, but this was found to be almost an endless task. After spending a whole day in counting reactions with the comparison lamp set at a given distance, it was usually found that the response induced by it was not equal to that induced by the given spectral color; so, after slightly increasing or decreasing the distance, as the results demanded, the experiment had to be continued for another day to see if the two beams were now equal; if they were not, the distance had again to be changed and another day spent, and so

[6] Field bees must be used. Young bees that have not yet become field bees are practically indifferent to light.

on. One was never quite sure when the true value had been obtained—never quite sure when to stop.

To avoid this difficulty the method was modified. Instead of varying the intensity of the white light on the ground glass in an effort to make its effect equal to that of the spectral light, the comparison lamp was left at a constant distance and its effect on the reactions of the bees was compared with the corresponding effect of each spectral color. The graduated head of the spectroscope was turned to indicate a given wave length—e. g., 698 m$\mu$—and, after the bees had been induced to assemble at the opposite end of the box, the beam from the comparison lamp and light of the wave length 698 m$\mu$ were thrown on the two screens simultaneously. The bees entering each of the tunnels were counted; then the bees were brought back to the starting point again and the process repeated until a total of 25 bees had entered the two tunnels. Then the graduated head was set for another wave length and the procedure repeated, and so on until each of the whole series of 14 different spectral colors had been compared with the constant white. Then the series was repeated, using the 14 spectral colors again, and so on for 20 series—i. e., until the total number of entrances (into both tunnels) observed in the comparison of each spectral color with the white amounted to 500.

For each wave length, in each series, a total of 25 bees, as has been said, entered the two tunnels. Only those entering the tunnel leading to the ground glass illuminated by the spectral color were recorded. To find the relative stimulative effect of light of a given wave length as compared with the stimulative effect of the white light used for comparison, the total number of bees recorded for a given wave length was divided by the corresponding total of those attracted to the white light; in other words, by the difference between 500 and the total recorded. For instance, in the 20 series, a total of 70 bees were attracted to the ground glass by light of wave length 431 m$\mu$. By dividing 70 by 430 (i. e., 500−70) the ratio 0.16 is derived as the relative stimulative effect of light of this wave length as compared with the white light taken as a standard. The results obtained are presented in Table 1. They indicate that, beginning with the shortest wave length and proceeding to the longest, the stimulative effect gradually increases to a maximum at 553 m$\mu$ and then decreases.

But a serious question arises here: Do the ratios obtained in this way represent the true relative stimulative effect of the respective wave lengths? For example, if the ratio for one wave length is twice that for another, is the stimulative effect of the former really twice that of the latter? At first thought the answer appears to be in the affirmative, but further consideration shows that these values may *not* truly represent the relative stimulative effect of the various wave lengths. For, according to the method used by Mast (*30*), already described, the true relative stimulative effects of diverse wave lengths are the relative intensities of white required to produce responses equal in magnitude to those produced by the several wave lengths used.

TABLE 1.—*Record of the number of bees attracted by light of selected wave lengths, and ratios of the totals for each wave length to the corresponding totals for the white light which was taken as the standard of comparison*

| Series | Number of bees attracted to light of wave length specified (in millimicrons) | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 431 | 451 | 471 | 492 | 512 | 532 | 553 | 574 | 595 | 615 | 636 | 657 | 677 | 698 |
| 1 | 3 | 6 | 6 | 8 | 11 | 10 | 11 | 15 | 11 | 7 | 4 | 4 | 3 | 1 |
| 2 | 2 | 7 | 6 | 9 | 10 | 8 | 12 | 8 | 6 | 9 | 3 | 4 | 6 | 1 |
| 3 | 6 | 4 | 7 | 6 | 14 | 10 | 11 | 8 | 9 | 6 | 8 | 4 | 3 | 1 |
| 4 | 7 | 1 | 6 | 9 | 10 | 13 | 13 | 14 | 8 | 6 | 4 | 5 | 2 | 5 |
| 5 | 0 | 5 | 9 | 8 | 8 | 12 | 13 | 14 | 9 | 10 | 7 | 4 | 6 | 3 |
| 6 | 2 | 4 | 5 | 10 | 8 | 15 | 11 | 14 | 14 | 9 | 7 | 2 | 0 | 2 |
| 7 | 5 | 4 | 8 | 7 | 12 | 18 | 16 | 16 | 9 | 10 | 6 | 4 | 4 | 0 |
| 8 | 4 | 4 | 9 | 8 | 10 | 15 | 14 | 13 | 15 | 6 | 5 | 5 | 2 | 0 |
| 9 | 6 | 9 | 8 | 10 | 8 | 10 | 14 | 11 | 14 | 9 | 8 | 6 | 3 | 2 |
| 10 | 5 | 6 | 9 | 10 | 15 | 13 | 14 | 13 | 12 | 13 | 7 | 3 | 2 | 0 |
| 11 | 4 | 5 | 10 | 11 | 13 | 10 | 12 | 12 | 8 | 9 | 6 | 4 | 3 | 3 |
| 12 | 3 | 4 | 7 | 12 | 7 | 10 | 13 | 13 | 11 | 8 | 7 | 6 | 5 | 0 |
| 13 | 6 | 7 | 8 | 11 | 10 | 10 | 14 | 13 | 9 | 9 | 7 | 3 | 2 | 1 |
| 14 | 5 | 3 | 9 | 8 | 11 | 11 | 12 | 8 | 14 | 8 | 5 | 5 | 4 | 2 |
| 15 | 1 | 3 | 6 | 8 | 10 | 9 | 13 | 9 | 11 | 9 | 7 | 4 | 5 | 6 |
| 16 | 0 | 6 | 7 | 10 | 13 | 13 | 12 | 9 | 8 | 5 | 4 | 5 | 3 | 2 |
| 17 | 2 | 7 | 4 | 11 | 14 | 13 | 11 | 11 | 11 | 10 | 4 | 5 | 3 | 4 |
| 18 | 4 | 5 | 5 | 9 | 9 | 6 | 10 | 10 | 13 | 13 | 3 | 3 | 2 | 2 |
| 19 | 4 | 6 | 7 | 11 | 8 | 12 | 13 | 13 | 10 | 6 | 5 | 1 | 4 | 1 |
| 20 | 1 | 3 | 6 | 6 | 10 | 10 | 11 | 14 | 11 | 9 | 4 | 3 | 3 | 3 |
| Total | 70 | 99 | 142 | 182 | 211 | 228 | 250 | 238 | 213 | 171 | 111 | 80 | 65 | 39 |
| Total attracted to white light | 430 | 401 | 358 | 318 | 289 | 272 | 250 | 262 | 287 | 329 | 389 | 420 | 435 | 461 |
| Ratio | 0.16 | 0.25 | 0.40 | 0.57 | 0.73 | 0.84 | 1.00 | 0.91 | 0.74 | 0.52 | 0.29 | 0.19 | 0.15 | 0.085 |

Consequently, the question that now arises is this: If a given wave length induces, for example, 25 per cent as great a response as a given white, how much will the white have to be reduced to bring about a response equal to that of the given wave length? Or, we may state the question in another way and ask, if a white beam be substituted for the spectral color, how intense will this white beam be, relative to the constant white, when it induces 25 per cent as many positive responses as the latter? In other words, what is the relation between the relative intensity of two beams of white light and the relative magnitude of the responses induced by them?

This relation was found without much difficulty. The apparatus used for this purpose was the same as that represented in Figure 1, except that for the spectroscope unit there was substituted another unit just like the comparison lamp and its container, so as to produce two beams of white light against the diffusion screens. The beam coming from the comparison lamp was left constant, while that coming from the new unit was varied in intensity through eight steps, ranging from approximately three times the intensity of the comparison lamp down to zero, either by substituting a more powerful lamp, by changing the distance of the lamp, or by interposing a neutral tint filter of carefully measured transmission, or, finally, by turning off the lamp entirely.

The experiment was conducted practically as has been described; that is, the bees, after being placed in the box and fed, were caused to assemble at the opening illuminated by the small pilot lamp (fig. 1, *c*), then the two lamps illuminating the pieces of ground glass at the opposite end of the box were turned on and the pilot lamp was turned off, after which the bees entering each of the two tunnels leading to the ground glasses were counted. The bees were now

again brought together at the starting point, by turning on the pilot lamp and extinguishing the other two; then the pilot lamp was turned off and the other lamps on, after which the bees entering each tunnel were again counted. The cycle was repeated again and again, new bees being used from time to time, as already described, until a total of from 500 to 2,000 bees had entered the two tunnels for each of the eight values of the variable illumination used.

Since the purpose of this experiment was to find the relation between the relative intensity of the variable beam and the relative number of bees going toward the spot illuminated by it, the results are tabulated as two ratios: (1) The ratio of the intensity of the variable to that of the constant beam, and (2) the resulting ratio of the number of bees attracted by the variable beam to the number attracted by the constant beam. The intensity ratios, for the eight different intensities of the variable beam used, are 2.98, 1.00, 0.50, 0.25, 0.11, 0.05, 0.01 and 0; the ratios of the effects on the bees corresponding to these are 1.67, 1.01, 0.85, 0.66, 0.50, 0.40, 0.20, and 0.09. These ratios and a summary of the observations on which they are based are presented in Table 2.

TABLE 2.—*The ratios of intensities of a variable beam of light to the intensity of a constant beam, tabulated for comparison with the corresponding ratios of the numbers of bees attracted to each light*

| Ratio of intensity of variable beam to that of constant beam | Total number of bees observed | Number of bees attracted by variable beam | Number of bees attracted by constant beam | Ratio of number of bees attracted by variable beam to number attracted by constant beam |
|---|---|---|---|---|
| 2.98 | 1,000 | 625 | 375 | 1.67 |
| 1.00 | 1,000 | 502 | 498 | 1.01 |
| .50 | 1,000 | 459 | 541 | .85 |
| .25 | 1,500 | 597 | 903 | .66 |
| .11 | 1,000 | 333 | 667 | .50 |
| .05 | 2,000 | 576 | 1,424 | .40 |
| .01 | 500 | 85 | 415 | .20 |
| 0 | 500 | 40 | 460 | .09 |

The data presented in Table 2 show clearly the following facts: When the two intensities of the pair are equal (column 1, ratio 1.00) the stimulative effect produced by each is practically the same (last column, ratio 1.01), as one would expect. But when the intensity of the variable beam is changed, the effect does not change proportionally; for example, when the intensity of the variable beam is decreased so that its ratio to that of the constant beam is 0.11 (first column), the effect produced decreases only to a ratio of 0.50 (last column). For unequal illumination the departure from direct proportionality is evident throughout. It will be observed that even when the intensity of the variable beam is reduced to zero (lamp turned off entirely), some bees enter this unlighted tunnel. This behavior is due partly to the activities of indifferent bees—bees which, after being confined for a little while, seem to lose their photopositiveness and simply roam aimlessly about, sometimes entering the unlighted tunnel; it is due partly also to the flaring shape of the

tunnels, which sometimes catch bees coming in from one side of the box toward the tunnel on the opposite side.

The relation between intensity of illumination with white light and magnitude of response on the part of the bees is brought out more clearly when the relative magnitude of response is plotted as a function of the relative intensity of the variable illumination which produced it. The resulting curve (fig. 2) is not a straight line, but is suggestive of a parabola; however, if the logarithms of the related variables are plotted, an approximately straight line results which correspondingly represents the equation

$$\log R = m \log I + b,$$

where $I$ is the ratio of the intensity of the variable white light to that of the constant white light, $R$ the ratio of the number of bees attracted by the variable light to the corresponding number attracted

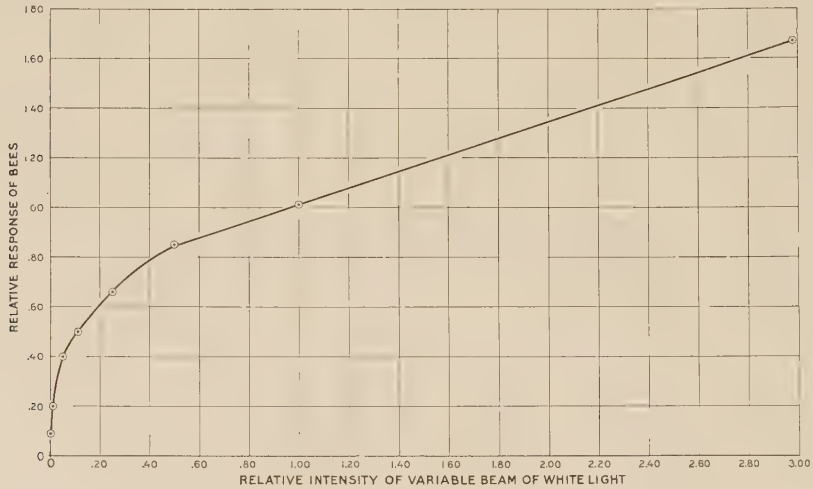


FIGURE 2.—Correlation of the relative intensity of a variable beam of white light and the relative number of bees apparently responding to it

by the constant light, $m$ the tangent of the angle of inclination, and $b$ the y intercept (a constant).

It may be pointed out, in passing, that neither does a straight line result when the relative response is plotted as a function of the logarithm of the relative intensity instead of the relative intensity itself; the resulting curve, shown in the lower part of Figure 3, makes it evident that the relation considered here is not in agreement with the Weber-Fechner law, according to which the magnitude of response increases as the logarithm of the stimulus. Only when the logarithms of both the relative intensity and the relative response are plotted does an approximately straight line result. This approximate proportionality between the logarithm of the stimulus of white light and that of the corresponding response on the part of the bees, a kind of by-product of the present research, seems worth a passing allusion for its mathematical interest. The line would have been perfectly, instead of approximately, straight if the curve in Figure 2 had been

exactly a parabola, and would have been inclined at a different angle. For the greater convenience and simplicity of plotting logarithms which are strictly positive quantities, and inasmuch as only the *relative* values of the intensities of light and of the observed reactions are concerned, the ratios plotted in Figure 2 have throughout been multiplied by 100, and the logarithms of the resulting products are those plotted in Figure 3.

It now becomes possible by the use of the curve shown in Figure 2 to find by graphic interpolation how intense a beam of white light must be, relative to the intensity of the beam from the comparison lamp (fig. 1), in order to produce the same effect as that produced by any one of the spectral colors. The ratio of response induced by the

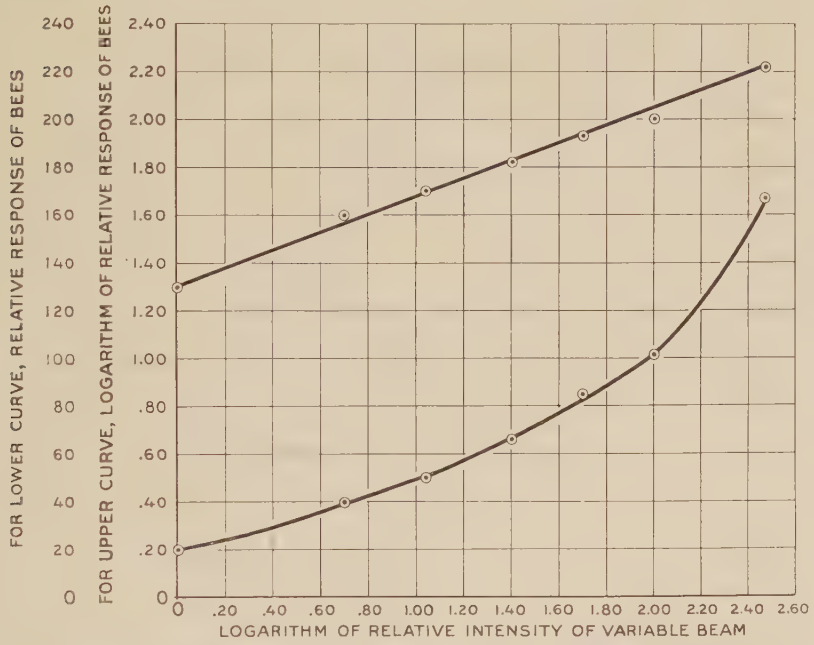


FIGURE 3.—Lower curve, relative response of bees as a function of logarithm of relative intensity of variable beam of white light; upper curve, approximately straight line found by plotting logarithm of relative response of bees as a function of logarithm of relative intensity

spectral region, for example, of wave length 451 mμ is found from Table 1 to be 0.25. Locating this value on the y axis, the corresponding relative intensity of white light is found by the curve to be approximately 0.022, as read off on the x axis. Similar values for the light of each of the 14 spectral bands used in this research were found by this method from a carefully drawn curve like the one in Figure 2 but made on a suitably large scale. In Table 3 are shown, in the first column, the wave lengths of the 14 spectral bands; in the second, the relative stimulative effect of their several colors, taken from the last line of Table 1; and in the third, their relative stimulative values in terms of the constant white illumination, as found by the method of graphic interpolation just described.

TABLE 3.—*Steps in the derivation of the relative stimulative efficiency of selected spectral colors in producing reactions of bees*

| Wave length | Relative stimulative effect [a] | Relative stimulative value [b] | Relative energy at slit of spectroscope [c] | Relative stimulative efficiency | Relative stimulative efficiency, with maximum at 100 |
|---|---|---|---|---|---|
| *Mμ* | | | | *Per cent* | *Per cent* |
| 431 | 0.16 | 0.005 | 0.18 | 2.78 | 10.11 |
| 451 | .25 | .022 | .4 | 5.50 | 20.00 |
| 471 | .40 | .060 | .8 | 7.50 | 27.27 |
| 492 | .57 | .163 | 1.2 | 13.58 | 49.38 |
| 512 | .73 | .330 | 1.8 | 18.33 | 66.65 |
| 532 | .84 | .525 | 2.5 | 21.00 | 76.36 |
| 553 | 1.00 | .990 | 3.6 | 27.50 | 100.00 |
| 574 | .91 | .700 | 4.7 | 14.89 | 54.15 |
| 595 | .74 | .345 | 6.4 | 5.39 | 19.60 |
| 615 | .52 | .125 | 8.0 | 1.56 | 5.67 |
| 636 | .29 | .030 | 10.1 | .30 | 1.09 |
| 657 | .19 | .009 | 12.8 | .07 | .25 |
| 677 | .15 | .004 | 16.0 | .025 | .09 |
| 698 | .085 | 0 | 19.5 | 0 | 0 |

[a] From last line of Table 1.
[b] Found by interpolation on the curve of relative response as a function of relative intensity of illumination. (Fig. 2.)
[c] Determined by W. W. Coblentz.

The values last named are those which are necessary for ascertaining the relative *efficiency* of each of these spectral colors, these relative efficiencies being the ultimate object of the research. They are found by dividing the relative stimulative values shown in column 3 by the relative expenditure of energy in the corresponding spectral color; the several quotients represent the relative efficiencies sought. The relative expenditure of energy in each of the 14 wave lengths used was determined for the writer by W. W. Coblentz, of the United States Bureau of Standards, with a delicate thermopile and galvanometer, and the results are shown in the fourth column of the table. In the fifth column are shown the relative stimulative efficiencies sought, the several quotients having been multiplied by 100 in order to be shown as percentages, and in the sixth column the same relative efficiencies after the maximum efficiency has been given an arbitrary value of 100 and the others a proportionate value; in both these columns the values are given as percentages. It will be seen that the efficiency is very low in the red, not attaining a value of 1 per cent of the maximum until the wave length 636 mμ is reached; from there it rises rather rapidly to a maximum at 553 mμ; from this point it decreases more gradually until at 431 mμ, the shortest wave length obtainable with the spectroscope used, the efficiency is approximately 10 per cent of the maximum.

The distribution of relative stimulative efficiency in the spectrum is made much more evident if these values are plotted as functions of their respective wave lengths and a curve drawn connecting the points. (Figure 4, solid line.)

A comparison of the curve for the bee with that for man, presented in Figure 4, shows that their respective maxima are at about the same wave length, but that the efficiency of the longer waves is greater for man than for bees, and the efficiency of the shorter waves less. The curve for man, as shown in the illustration, has been drawn from

data compiled by Gibson and Tyndall (*12, p. 173*), of the United States Bureau of Standards.

### CONCLUSIONS

The upper limit of the spectrum for the honeybee extends to at least wave length 677 mμ. Kühn (*22, p. 799*) found evidence of its extent to only about 650 mμ. The difference between these assigned limits is probably due to the difference in intensity of the spectral light used in the two sets of experiments. The lower limit was not ascertained in the research here reported, but according to Kühn it extends to at least 313 mμ.

The point of maximal stimulative efficiency is at about 553 mμ, which corresponds rather closely with that for man. From this point the efficiency decreases more rapidly for bees than for man toward the

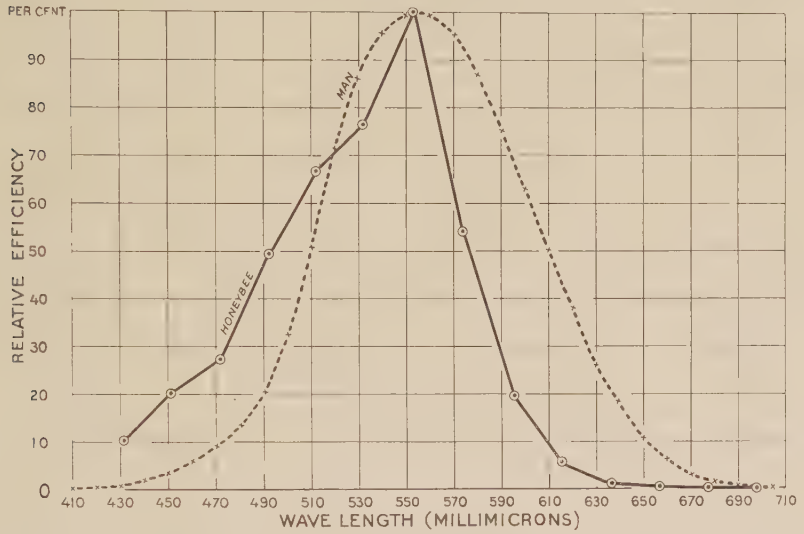


FIGURE 4.—The distribution of relative stimulative efficiency in the spectrum for the honeybee compared with similar distribution in that for man

longer wave lengths, but more slowly than for man toward the shorter wave lengths, being at 431 mμ still fully 10 per cent of the maximum.

Untrained bees, when allowed to walk toward two sources of light of the same quality, placed near together at the end of a rectangular box, go to the brighter more often than to the fainter, but not in direct proportion to the relative brightness of the two. The curve representing the relation between relative brightness (energy) and relative magnitude of response is a polynomial one, of such form that the curve showing the relation between the logarithms of the two related variables is an approximately straight line.

## II. CHROMA VISION OF THE HONEYBEE

### DISCUSSION OF TERMS

In almost any paper involving the subject of light and color it is necessary to state clearly the sense in which various terms are to be used. This need arises from the lack of agreement among present-

day workers in the field of optics, human psychology, and general physiology as to the meaning of these terms.

A fundamental distinction is to be made between the terms "light" and "color;" the former is the name of a form of energy, entirely objective, while the latter is the name of a sensation, entirely subjective.

Light has three attributes—brightness, wave length, and purity. Brightness refers to the intensity of illumination as measured in some physical unit such as meter candles or ergs per square centimeter per second. In this paper the term is used synonymously with intensity.

Wave length refers to the dominant wave length of the portion of the spectrum under consideration; in practice it is usually impossible to obtain light of a single wave length. The unit of measurement here used is the millimicron.

Purity refers to the proportion of white light which is, in a given instance, mixed with the spectral light in question; the less the admixture of white light the greater the purity.

Likewise, color has three attributes—brilliance, hue, and saturation. We may, however, combine the last two, as will be done in this paper, and say that color has the two attributes, brilliance and chroma.

Brilliance is that attribute of a color which enables it to be classified as equivalent to some member of a series of grays, ranging between black and white. It is the quantitative aspect of color.

Chroma involves the hue—that is, the redness, yellowness, greenness, blueness, etc., of a color—together with the distinctness or vividness of the hue. It is the qualitative aspect of color.

Color, then, is merely a subjective phenomenon; a sensation that arises from the activity of the photoreceptors and their attached nervous mechanism. It includes the sensations not only of chroma (red, yellow, green, blue, and all combinations of these, for the human eye) but also of gray (the whole series from black to white, including the latter). The meaning of these terms becomes more evident if they are viewed in tabular form. The following arrangement of terms here discussed is a modification of one presented by the Progress committee on spectrophotometry for 1922–3 of the Optical Society of America (*33*):

Light (objective) evokes the sensation of color (subjective).
Brightness evokes the sensation of brilliance.
Wave length, Purity } evoke the sensation of chroma { hue, saturation.

If these definitions are adhered to, it will be seen that the terms "color blindness" and "color vision" lose entirely their usual meanings, the former coming to mean entire blindness, and the latter simply light vision; hence in this paper the terms "chroma blindness" and "chroma vision" will be used to express what is ordinarily meant by color blindness and color vision, respectively.

Chroma vision[7] may be defined, then, as the ability of an animal to distinguish between chromas of the same brilliance.

It may be argued that the terms "color," "brilliance," and "chroma," which describe purely human sensations, should not be used when referring to other animals than man, because we do not know what

[7] The use of the term "chroma" to avoid the ambiguities in the meaning of color, has been advocated by Ladd-Franklin (*25*) and Troland (*35*).

kind of photic sensations they have, if, indeed, they have any. That is true, of course, but as a matter of fact, even among human beings, no individual knows exactly how light appears to another individual, and yet we find the terms convenient in talking about these sensations. Likewise, in this paper, the terms are used only for convenience, and it is to be understood that there is no intention of attributing to insects the light sensations of human beings. When, for example, the writer speaks of bees being able to distinguish a blue from all shades of gray, he means colors that are called blue and gray by human beings, and no assumption is made as to what sensations they give to bees.

## REVIEW OF LITERATURE

The method which has always been used in investigating chroma vision of bees is the so-called training method, although several other methods have been used for other animals.[8] The method consists essentially of two procedures: (1) The training of the bee to come for food to a place where food is associated with a given chroma, and (2) the testing of the bee, by some change in the layout of the experiment, to see if it can select from other colors (i. e., chromas or grays) of equal brilliance the particular chroma used in training.

The training of bees to come to almost any desired experimentally arranged set-up is usually not difficult, neither is the evidence that bees select a given chroma from other colors difficult to obtain. But it is very difficult to make sure that at least one of the test colors is of the same brilliance to the bee as the training chroma.

Since chroma vision is, by definition, the ability to distinguish between chromas of equal brilliance, the question persistently arises in a critical review of previous experiments, were the colors used in the tests of the same brilliance to the bees as were the chromas used in the training?

Lubbock (*1*) and his contemporaries clearly established the fact that bees and certain other insects can under certain conditions distinguish one chroma from another, but they did not ascertain whether this distinction takes place on the basis of chroma alone or on the basis of relative brilliance; that is, they did not clearly distinguish chroma vision from brightness vision. Forel, however, recognized the fact that the mere ability to distinguish one chromed object from another is not a proof of chroma vision unless the objects are at the same time equally brilliant to the insect. He attempted (*5, p. 181*) to test the ability of bees to distinguish a given color to which they were trained from a number of grays of different brightness, but so many bees came to his dishes for food that the experiment failed.

Von Frisch (*6, 7*), however, carried out experiments in which this sort of procedure was successful. He set out in the vicinity of a hive a series of colored squares of paper, arranged after the manner of a checkerboard, consisting usually of one chromed paper (of the so-called Hering series), about 15 by 15 cm., and from 15 to 31 gray papers each of the same size but different in brightness, varying in approximately equal steps (for the human eye) from white to black (*6*). During the training period he placed on the chromed paper a watch glass containing sugar water and on each of the grays an empty watch glass. The position of the chromed paper was changed fre-

[8] A list of these methods, with bibliography, is given by Kühn (*21*).

quently to avoid training in reference to location. After a training period of from a few hours to several days the assemblage of squares was exchanged for another with fresh papers and clean watch glasses, all of which, however, were now empty. The result was that the bees came flocking to the chromed paper and practically disregarded the grays. This was also true when none of the papers carried watch glasses, and even when the grays carried watch glasses containing food while the chromed paper carried an empty watch glass. The chromed paper must have stimulated the bees differently, then, from any of the grays which were used, and since the grays varied in brightness from black to white, Von Frisch concluded that this difference in stimulation must have been due to difference in chroma, especially since he found that the bees could not distinguish between the grays.

Severe criticism of Von Frisch's work was made by Von Hess (*17*), who pointed out principally the lack of consideration which Von Frisch has given to the bees' sense of smell. Von Hess went so far as to obtain samples of the different dyes used in the Hering papers and noted that some of them were distinctly different from others in odor—even to man. He made a number of experiments with these papers, in which he used a plate of glass to cover them and claims to have obtained no evidence at all of chroma vision. For example, he made a "spectrum" consisting of 185 chromed papers ranging from red to blue, in small steps, so as to give the appearance of a prismatic spectrum. After "training" (Von Hess always put "Dressur" in quotation marks) bees to yellow for several days, he set out this whole "spectrum" covered with glass, on which he made a streak of honey running down the middle of the "spectrum" for its entire length. Bees did not collect first on the yellow but came indiscriminately and collected more or less uniformly along the whole streak. Von Hess therefore flatly contradicts the conclusion that bees possess chroma vision.

Von Frisch then modified some of his experiments in an attempt to meet Von Hess's criticisms. For example, he eliminated the possibility of training to a particular odor carried by the papers, by covering the whole series with a glass plate; this precaution made no significant change in the results. He even sealed papers within glass tubes and obtained the same results. He again (*7*) concludes, therefore, that bees possess chroma vision.

While this conclusion of Von Frisch thus seems to be founded on sound experimental results, it is valid only if the brilliance of each of the chromed papers was, for the bees, equal to that of some one of the grays. But it is by no means certain that this condition obtains, for it is possible that the chromed papers may have been more brilliant than any of the grays, and, indeed, than even the white, This has been ably pointed out by Lutz (*28*), who recalls a fact stated many times by Von Hess and others, that other animals may not have the same limits of perception in regard to wave length as human beings have. That is, it is entirely possible that the chromed papers used by Von Frisch reflected ultra-violet in so much greater amounts than any of the grays that to an animal relatively highly sensitive to ultra-violet these papers would appear brighter than even the white. As a matter of fact, Lutz shows that bees and several other insects are relatively much more sensitive to ultra-violet than man—a fact that has been suspected ever since Lubbock (*1*) demonstrated the sensitivity of ants

to ultra-violet. Lutz then tested the Hering papers used by Von Frisch and found most of them to reflect some ultra-violet. He did not have samples of the grays to test, hence could make no comparison of the ultra-violet reflection of grays and chromas. The fact that in some experiments Von Frisch used a plate of glass to cover his papers does not entirely exclude the effect of ultra-violet, since ordinary glass often transmits down to the wave length 320 mμ.

Lutz, then, while concluding that Von Frisch is probably correct in ascribing chroma vision to bees, does maintain that he has not proved it. He said:

> Hess may be right in believing that insects are totally color-blind. Probably Von Frisch is more nearly correct in saying that they can distinguish all of the colors except red and certain greens as colors * * *.

Kühn (*20*, *22*) performed some experiments designed to meet such criticisms as those made by Lutz. He made several tests, one of the simplest of which may be described as follows: Bees were trained to come for food into a semidark room and there to congregate at a narrow trough filled with sugar water and illuminated from above by a narrow streak of spectral light—e. g., from the blue-green region. After a sufficient period of training, the bees congregated on this streak of light even when the trough of food was removed. If now another streak of light of the same wave length but different intensity was thrown diagonally across this streak, after the manner of the letter X, the bees always collected on the more intense of the two streaks, no matter to which they had been trained. But when a streak of white light, taken directly from the same source as that used to produce the spectral streak, was thrown across the training streak, the bees did not collect on the white but continued to collect on the spectral streak. This he regards as proof that the spectral streak was for the bees qualitatively different from the white streak. But this is true only if the white streak was more brilliant to the bees than the other. On first thought it appears obvious that a beam of white light should always be more brilliant than any of the monochromatic constituents of that white beam. But Lubbock (*1*) long ago demonstrated that this does not necessarily obtain; he showed that white light after it has been modified by being passed through a certain filter is more stimulative to Daphnia than the same white light unfiltered. Hence it is possible that in Kühn's experiment the bees continued to flock to the spectral color merely because it was more brilliant to them than the white; in other words, it had a greater quantitative effect. From these facts it seems evident that the problem as to the presence of chroma vision in bees is open to further investigation.

## METHODS AND RESULTS

In order to test the presence of chroma vision in bees it was decided to do three things: (1) Select a series of filters transmitting different portions of the spectrum, (2) ascertain the relative brilliance to bees of the light transmitted by each, and (3) ascertain by experiments in training whether or not bees can select a given one of these chromas from the others after all have been made equal in brilliance.

The filters selected were four made of glass and a fifth, consisting of a glass cell 3 cm. deep, filled with a solution of potassium dichromate (24 gm. per liter). The transmission curves of these filters are presented in Figure 5. The height of the peak of each curve repre-

sents its relative total transmission,[9] and the points of intersection of each with the base line represent with fair accuracy its limits of wave length as determined by observing through a spectroscope the lines of the mercury-vapor spectrum which it transmits,[9] and by the use of spectrograph photographs (*10*). The shapes of the various curves are only approximate, since the transmission for various wave lengths was not determined, but the shapes agree with those of curves for similar glasses, or even identical glasses but of different thickness, as given, for example, by Gibson, Tyndall, and McNicholas (*13*). Since all of these filters when used alone transmit a large proportion of infra-red rays, a cell containing a solution of copper sulphate (19 gm. per liter) 3 cm. deep was always used in connection with them to screen out these rays. A curve for the combined solutions of copper sulphate and potassium dichromate is given by Gibson (*11, p. 274*).[10]

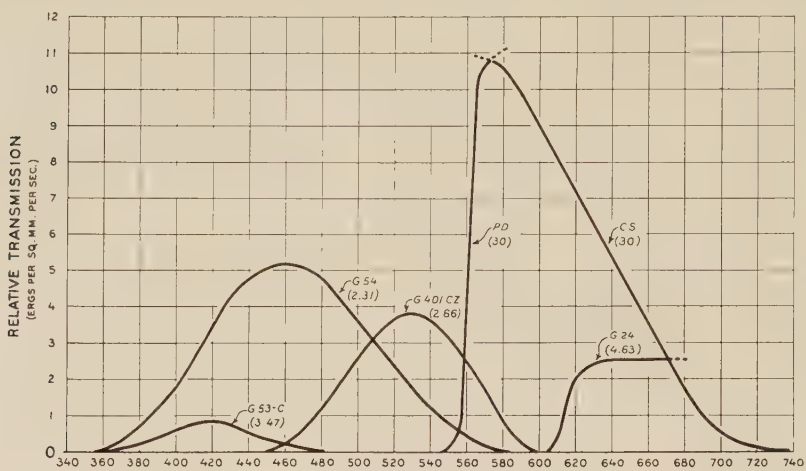


FIGURE 5.—Transmission curves for the color filters used in the study of chroma vision in bees: G53–C transmits violet; G54, blue; G401CZ, green; and G24, red; PD is the curve for potassium dichromate and CS that for copper sulphate. The dimensions in parentheses are the thicknesses (in millimeters) of the filters used

It is, of course, very difficult to find five color filters all of which transmit entirely separate and distinct portions of the spectrum. It will be observed here, for instance, that the yellow filter transmits at the same time all that the red filter does, and the blue all that the violet does. And yet these filters appear unmistakably different to the normal human eye. The reason the blue appears different from the violet is, obviously, because the major portion of the light transmitted by one is in the region we call blue and by the other in the region we call violet. If a bee can distinguish one of these from the other after they have been made equal in brilliance to the bee, we may say with confidence that the bee possesses chroma vision, for even though the transmission curves overlap, whatever difference there is, under these conditions, must be due to chroma.

[9] Kindly determined for the writer by R. Stair in the laboratory of W. W. Coblentz.

[10] The curve in the reference cited is for a solution of copper sulphate ($CuSO_4.5H_2O$) containing 57.0 gm. per liter and for a solution of potassium dichromate ($K_2Cr_2O_7$) containing 72.0 gm. per liter, each in a cell 10 mm. thick. Since in the present investigation the glass cells were 3 cm. thick, the concentration was reduced by two-thirds, giving, according to information personally furnished the writer by Gibson, the same curve as that shown in the reference.

The chromas having been selected, the next problem was to find their relative stimulative effect (relative brilliance) for the bees. One of the main difficulties in doing this proved to be the finding of a suitable reaction to measure—by no means an easy task. It was found, for instance, that when the bees were placed in the intersection of two wide beams of light their reactions could not be measured accurately because of the bees' excitability and rapid movements. Likewise, the ratio of the numbers that congregated at the two ends of a box into each end of which a beam of light entered—although this method was used by Von Hess (*18*) with apparent success—was found in these experiments not to be a sufficiently delicate measure of the relative brilliance of the respective beams, because of the great restlessness of the bees and the ready modification of their behavior through inability to escape, and other incidental factors.

A much more satisfactory measure of the relative stimulative effect was found in the reactions of individual bees to two beams of light coming from opposite directions, as these reactions were observed in the apparatus now to be described. (Fig. 6.) A beam of light from a 400-watt projection lamp passes first through a solution of copper sulphate (to remove the infra-red rays) and then through a pair of rotating sectors, one variable in position with respect to the other. (Fig. 7.) The upper half of the beam is intercepted by only the larger of the two rotating disks *d* but the lower half is intercepted by both. When the sectors of the two disks are made to coincide with each other and are then rotated together, the light intensity of the lower half and that of the upper half of the beam are identical; but by turning the smaller disk *c* with respect to the larger and rotating them together the intensity of the lower half of the beam can be diminished to any desired degree until, when the sectors are exactly opposite in position, it is completely screened out. The position of the smaller disk with respect to the larger can be varied by means of a suitable knurled collar, graduated in percentage.[11] After passing the sectors (fig. 6), the upper half of the beam is deflected by a mirror and proceeds at an angle of 90° to its former direction, while the lower half of the beam is allowed to pass on. The two beams, now proceeding in directions at right angles to each other, are caught at equal distances from the first mirror by other mirrors which turn

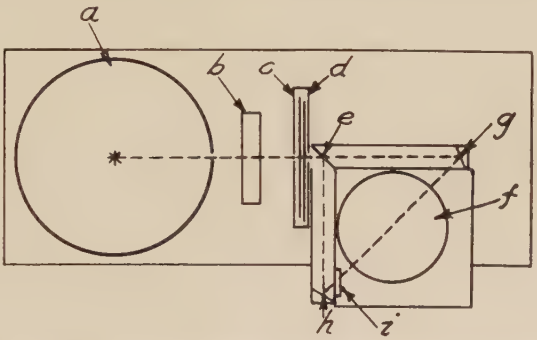


FIGURE 6.—Explanatory diagram of apparatus used to ascertain the relative stimulative effect on honeybees of transmitted light of various chromas: *a*, 400-watt lamp, the source of illumination; *b*, glass cell containing a solution of copper sulphate, for screening out infra-red rays; *c*, *d*, two rotating sectors, adjustable with respect to each other, for transmitting two beams of light of variable relative intensity; *e*, mirror for reflecting one of the two beams at a right angle; *f*, cover (inverted) of a large Petri dish, for containing bees under observation; *g*, *h*, mirrors for reflecting the two beams into two opposite sides of the inclosure *f*; *i*, light filter

[11] The rotating sectors and the lamp house of this apparatus are a part of the Keuffel and Esser color analyzer.

them directly toward each other. The beams now pass through light filters, if desired, and enter the opposite sides of an inverted cover of a large Petri dish, under which are imprisoned from one to three bees. Since the apparatus is set up in a dark room, with the lamp house well shielded, these two beams are practically the only light which strikes the bees. Figure 8, from a photograph, shows the apparatus as a whole, except the Petri dish and the top of the lamp house.

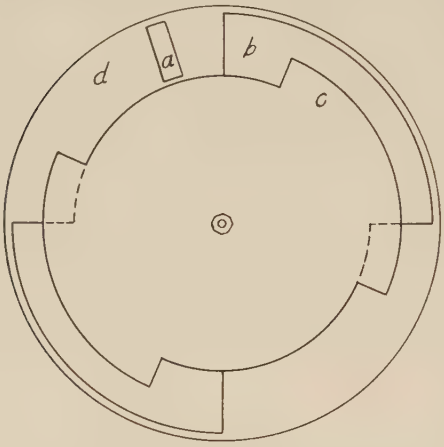


FIGURE 7.—Diagram of rotating sectors used to vary the relative intensity of the upper and lower halves of a beam of light: *a*, The aperture through which the beam passes; *b*, the larger rotating disk, which always intercepts the whole beam, reducing its intensity by one-half; *c*, the smaller rotating disk, its position variable with respect to the other, which intercepts only the lower half of the beam of light, reducing its intensity to any additional degree desired, according to its position with respect to the larger disk; *d*, the housing which incloses the disks

It was found that under these conditions the bees walk hurriedly around under the glass dish, and whenever they come to the spot on the side where a beam of light enters they pause and start as if to walk up the side of the dish. After an attempt or two they pass on until they come again to a spot where a beam enters. When the two beams are decidedly unequal in intensity the bees attempt to escape most often at the more intense beam; by increasing the intensity of the weaker beam, however, a point is reached at which this beam induces about as many of

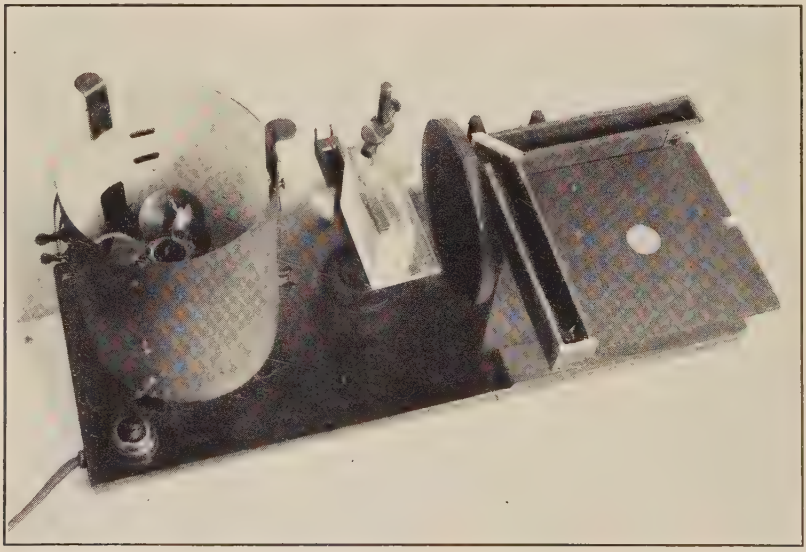

FIGURE 8.—General view, from a photograph, of the apparatus illustrated in Figure 6. The Petri dish and the top of the lamp house are lacking

these peculiar reactions as the other. This is then considered the point at which the two are equal in brillance for the bee.

The procedure, then, was first to place one of the chromed[12] filters, mentioned above in the text and in connection with Figure 5, in the constant beam, leaving the variable beam white. A count of the reactions to each then indicated whether the chromed or the white beam was the more stimulative to the bees. If the white was the more stimulative its intensity was reduced, if the less stimulative, it was increased, after which, in either case, a count was again made. In this way, after making a series of tests, a percentage of the total white available could be found which induced approximately the same number of reactions as a given chromed beam. This percentage, obtained for each filter, was regarded as a representation of the relative stimulative effect (relative brilliance) of the light produced by each filter.

It was found that the exact percentage of white required to equalize a given chromed beam in stimulative effect was very difficult to ascertain accurately. The difficulty may have been due to an insufficiently delicate means of measuring the reactions, but it was probably due rather to an inability of the bees themselves to recognize differences in brilliance between a chromed and a white beam unless those differences are of considerable magnitude.

In the method finally chosen for finding these values the percentage of available white used was first made so low that in most tests it definitely induced fewer reactions than the chromed beam. Then the intensity of the white was increased by small steps until it definitely induced more reactions than the chromed beam. By putting down in order the results of these tests, a point could be chosen which seemed to represent with fair accuracy the percentage of white which just equaled the chroma in stimulative effect. Thus, in the experiment in which green was compared with white, white at the intensity of 15 per cent of the total white available induced 48 per cent of the total reactions; at the intensity of 20 per cent it induced 45 per cent of the total reactions; and with the percentage of white increased at suitably chosen steps, fully set forth in Table 4, the percentage induced of the total reactions increased correspondingly to 58 per cent, both for 40 and for 56 per cent of the maximum available white. In this series it appears that any percentage of white between 15 per cent, or perhaps lower, and 35 per cent was approximately as stimulative to the bees as green. There is an indication of a gradual rise, however, so that the most probable value for equal stimulative effect seems to fall at from 28 to 30 per cent, and the latter figure was adopted.

These results and those obtained for the other chromas are presented in Table 4. The percentage of white required to equal the effect of blue seemed to lie between 7 and 25, with the mean at about 20, and for the yellow the percentage seemed to lie between 15 and 30, with the mean also at about 20. For the violet and red the brilliance was very low and hard to measure. For the former the mean percentage of white required was about 2, and for the latter between one-fourth and one-half, and the larger fraction was chosen.

[12] In accordance with the definition of chroma discussed at the beginning of Part II, a chromed filter, chromed beam, etc., is any filter, beam, etc., whose color is some other than a shade of gray.

TABLE 4.—*Summary of experiments performed to find the relative percentage of white light required to equal in stimulative effect the light transmitted by five light filters*

| Color of filter | Available white used | Bees used | Reactions | Reactions induced by white light | Color of filter | Available white used | Bees used | Reactions | Reactions induced by white light |
|---|---|---|---|---|---|---|---|---|---|
| | *Percent* | *Number* | *Number* | *Per cent* | | *Percent* | *Number* | *Number* | *Per cent* |
| Green | 15 | 6 | 500 | 48 | Yellow | 15 | 5 | 600 | 51 |
| | 20 | 5 | 150 | 45 | | [a] 20 | 6 | 500 | 47 |
| | 25 | 2 | 150 | 47 | | 25 | 10 | 1,200 | 51 |
| | 28 | 4 | 300 | 48 | | 30 | 4 | 550 | 53 |
| | [a] 30 | 5 | 500 | 51 | | 35 | 6 | 650 | 53 |
| | 35 | 10 | 750 | 51 | | 40 | 4 | 350 | 52 |
| | 40 | 2 | 50 | 58 | | 50 | 2 | 150 | 59 |
| | 56 | 2 | 50 | 58 | Violet | 1 | 8 | 350 | 41 |
| Blue | 7 | 3 | 200 | 49 | | [a] 2 | 10 | 725 | 55 |
| | 10 | 3 | 200 | 50 | | 5 | 1 | 50 | 66 |
| | 15 | 9 | 550 | 50 | Red | ¼ | 2 | 25 | 28 |
| | [a] 20 | 3 | 500 | 49 | | [a] ½ | 8 | 275 | 62 |
| | 25 | 9 | 825 | 50 | | 1 | 2 | 50 | 82 |
| | 30 | 4 | 350 | 55 | | 7 | 2 | 25 | 84 |
| | 35 | 2 | 200 | 52 | | | | | |
| | 48 | 3 | 100 | 56 | | | | | |

[a] Chosen as being equal to the chromed light in each series.

Multiplying these percentages by 2 to eliminate the fraction, we may say that the relative brilliance of these chromas for bees stands approximately in the numerical ratio of green 60, blue 40, yellow 40, violet 4, and red 1, with the understanding that these are merely mean values. They do not represent the relative efficiency of the chromas considered, but rather the relative stimulative effect of the chromas on untrained bees.

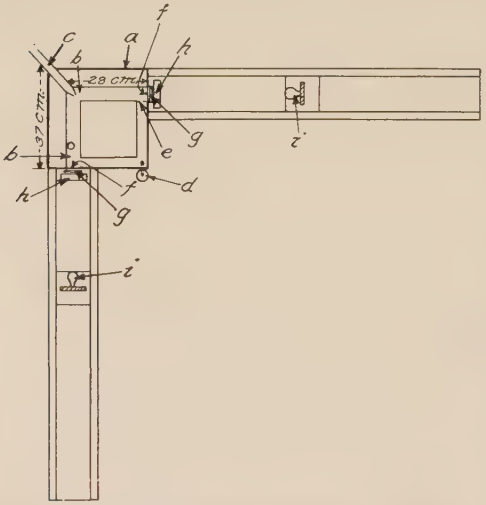


FIGURE 9.—Diagram of apparatus for testing the ability of bees to distinguish between chromas: *a*, Box 37 cm. square; *b*, *b*, glass-covered tunnels, about 3 cm. wide by 2 cm. deep, within and along the sides of a square 28 by 28 cm. outside; *c*, passage between tunnels and exterior of building, for entrance and exit of bees; *d*, feeder; *e*, wire screen; *f*, *f*, diffusion screens of ground glass, each covering a rectangular aperture 15 by 30 mm. in size; *g*, *g*, light filters; *h*, *h*, glass cells for holding solution of copper sulphate; *i*, *i*, 100-watt electric bulbs, for illuminating apertures covered by the diffusion screens, adjustable for distance by means of carriers sliding on tracks

After these values had been found, the next procedure was to ascertain, by training and testing, whether or not bees can select any given one of these chromas from any other one when the two are made equal in brilliance; that is, equal in equivalent percentages of the available white light used with the apparatus just described.

The apparatus (fig. 9) used for this purpose consisted essentially of a square box, measuring 37 cm. on each side, with a passage for the entrance and exit of bees in one corner and a feeder in the opposite corner. Two glass-covered passageways led from the entrance in opposite

directions, leaving at right angles to each other, and following the sides of the box around to the feeder. At a point in each of the two opposite sides of the box, visible from the entrance, a rectangular opening 15 by 30 mm. was made, through which a beam of light entered from a 100-watt lamp placed in a covered tunnel outside. From the inner end of the entrance the two openings were visible in directions at right angles to each other. The intensity of either beam could be varied by changing the distance of the corresponding lamp. A ground-glass diffusion screen was placed over each rectangular opening; as the openings were immovable and constantly equal in size and in distance from the inner end of the entrance, any movement of the lamps caused no variation in the size of the images. The chromed filters were placed just back of the diffusion screens. The whole apparatus was placed in a dark room, and only a narrow tunnel connected it with the exterior. Enough light came from the lamps through the light filters and diffusion screens to enable an observer to watch the bees in the tunnels near the entrance.

The first step in using the apparatus was to get the bees voluntarily to enter the box. This required considerable patience but offered no great difficulties. A dish of sugar water was placed out, preferably in the early morning, until it was found by bees. The first visitor, on its return to the hive, stimulated a number of its companions to rush out in all directions, and some of them came to the food. On their return to the hive they stimulated others, and in a short time a large squad was built up, the members of which made regular trips between feeding dish and hive. Now the dish was moved toward the training box, at first only a few centimeters at a time, then, as the bees became accustomed to searching (apparently) for it, several paces at a time, letting it remain in each new location until most of the bees had come to it there. When, finally, the entrance leading to the training box was reached, drops of sugar water were placed consecutively every few centimeters along the circuitous route leading from the exterior to the feeder in the far corner of the training box. As soon as the bees had removed one drop they proceeded to the next, until finally a few succeeded in reaching the feeder. In doing this they had, first, to go from bright daylight into a dark tunnel leading from the outside to the box itself, located in the dark room, then turn obliquely and walk down a brightly lighted passageway toward one lamp or the other, then turn at right angles into a dark passageway, and finally reach the feeder in the corner. The return trip involved the reverse of this procedure. This series of reactions is much more complex than the reactions used in taking nectar from a flower under natural conditions, and represents, evidently, a considerable modification in behavior. In other words, the bees following this route were learning a new set of facts, differing considerably from those of their usual experience in the hive and in the open air.

Under these circumstances the few bees that first learned the way to the feeder appeared to stimulate their companions, so that, if the food was abundant, the squad of bees became, after a few hours, so large that it was impossible to count them. And not only that, but they developed the so-called "robbing fever," under the influence of which they seemed to lose their usual well-marked ability to learn; instead, they scrambled over one another in what resembled a frenzy of hit-or-miss efforts to find the feeder. To prevent the coming of

such large numbers, one of the most successful methods found[13] was to reduce the size of the opening of the feeder to such dimensions that only one bee could feed at a time. The feeder devised for this purpose is diagramed in Figure 10. The sugar sirup in the inverted bottle *a* runs down through the tube *b* into the cup *c*. From here the sirup runs around through the smaller tube *d* to the small feeding cup *e* until both cups *c* and *e* are about half full. As soon as the level of the sirup in *e*, and consequently in *c*, rises to such a height that the lower end of tube *b* is closed, the entrance of any more air into tube *b* is prevented, and consequently no more sirup runs out of bottle *a*. As soon, however, as a bee feeding at the cup *e* reduces the level of the sirup in *e* and *c* to a point where more air can enter tube *b*, more sirup runs down from bottle *a* and the level in *e* and *c* rises again. Thus, as long as there is sirup in bottle *a*, there will be a supply also at the cup *e*, and it will be fed down only as fast as it is taken away by the bees.

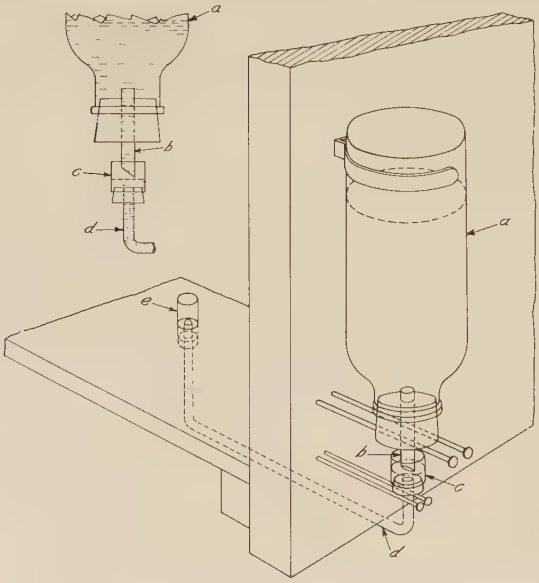


FIGURE 10.—Feeder used in apparatus for testing the ability of bees to distinguish between chromas: *a*, Inverted bottle used as reservoir for sugar sirup; *b*, glass tube conducting sirup into open cup *c*; *d*, glass tube connecting *c* and *e*, the sirup in the two being always at the same level; *e*, feeding cup, made of ¼-inch glass tubing, admitting the head and thorax of one bee at a time

The particular point of interest here is the fact that the cup *e* is large enough to admit the head and thorax of only one bee at a time. This, of course, was an effectual check on the rate at which a squad of bees could obtain food. By the aid of this contrivance and by using a suitable concentration of sugar sirup the rate at which bees came could be reduced almost as much as desired, because the time required for a bee to feed increases with increased concentration. The sirup used in these experiments contained about 2 parts of sugar to 1 of water (by volume). With this arrangement a small squad of bees, usually not more than 15, made regular trips from the hives to the feeder and back, entering and leaving the box at the rate of about one bee a minute. There was an appearance of eagerness and purpose in their behavior, but no frenzy. Usually there were five or so crowding around at all times, ready to enter the opening of the feeder. The bees were at first marked on the back with a mixture of orange G in shellac in order to make it possible to identify the trained bees, but this precaution was found to be superfluous because very few novices came to the box, and these could be distinguished at once by their hesitation and lack of orientation. How-

[13] Suggested to the writer by Jas. I. Hambleton.

ever, the few novices usually learned the route after a while, and their number balanced, approximately, the number that died, so that the squad continued roughly uniform in size.

After a regular squad had been formed and its members were able to find the way to the feeder, a chromed filter was placed behind each diffusion screen and the distance of each lamp from the corresponding screen was so adjusted that the two beams had the same brilliance, according to the values already obtained and recorded in Table 4, and the training then began. Suppose it is desired to train the bees to associate with food the beam of light at the left, as the reader looks at Figure 9. The food is to be obtained only at the feeder in the corner of the box opposite the entrance. In order to reach it the bee, on entering, must walk for half the distance down a passageway directly toward one lamp or the other, then make a right-angled turn and walk an equal distance through a dark passageway until the feeder is reached. But a wire screen is placed in the dark portion of the passageway at the right, so that the bee can finally reach the food only by taking the other passage. After experiencing failure by way of the right but success by way of the left for a period of a day or two, most of the bees take the correct route without hesitation immediately on entering the box. It may be observed that the opening of the feeder is placed in the corner of the box opposite the entrance, so that any odor emanating from the food will be equally present in both passages.

Out of a total number of bees observed as they enter the box, the number taking the correct route—i. e., the route leading to the food—gives the "total per cent trained." They are presumably trained to position, but they may or may not be trained to chroma; that is what is now to be ascertained. To do this the position of the two beams of light is exactly reversed by interchanging the filters and adjusting the distances of the lamps accordingly, but the wire screen is left unchanged. The percentage of the original total number continuing to take the route leading to the feeder after this reversal gives the "per cent trained to position only;" that is, they do not follow the training chroma but continue to go to the old location; they are trained to position rather than chroma. Subtracting the "per cent trained to position only" from the "total per cent trained," we obtain the "per cent trained to chroma."

An example will make the procedure clear: Date, October 21, 1927; training chroma (at left), blue; opposite chroma, violet; length of training period, four hours. At the end of these four hours of training the observer took his stand at the entrance to the box and watched the reactions of 10 bees as they entered. Of these, 8 turned at once toward the blue (i. e., toward the left) and went directly around to the feeder in the far corner. Hence the "total per cent trained" is 80. Now the chromas were interchanged, blue at the right, violet at the left, wire screen still at the right, and the next 10 bees that entered were observed. Of these, 5 turned to the left as the 8 had done before, although now the color at the left was violet instead of blue. Evidently these 5 were not trained to chroma, but to position only; hence the "per cent trained to position only" is 50. Subtracting this latter figure from 80, the "total per cent trained," we obtain 30 as the "per cent trained to chroma."

This method of calculating the net percentage trained eliminates the possibility of including bees which are trained merely to location and not to chroma. It is of course apparent that in this apparatus the bees depend in the training process not only on their sense of sight but also on their sense of direction; that is, they become trained to turn in a *right or left direction* as well as toward a given quality of light. Hence, after a training period, when the position of the two chromed beams is exchanged, no bees will follow the training chroma to its new location unless the association with light is stronger for them than the association with direction. The values obtained, then, for percentage trained to chroma will always represent the training to light which exceeded the training to direction. For this reason, even small percentages of training to chroma are to be regarded as significant.

The results of the 23 experiments performed are presented in Table 5. It will be observed, in the column "Per cent trained to chroma," *that in every experiment except three there was distinct selection of the chroma associated with the food* (the training chroma). That is, after being trained to blue, for example, in the pair blue versus violet, the bees followed this blue when its position was changed, although as far as its nonchromatic brilliance was concerned it must have been indistinguishable to them from the violet. Selection occurred irrespective of which chroma of the pair was used as the training chroma—i. e., as the chroma toward which the bees had to travel during the training period in order to reach the feeder.

TABLE 5.—*Summary of results of a series of experiments performed to test the ability of bees, after they had been trained to associate color with food, to distinguish between chromas of equal stimulative influence*

| Training chroma | Opposite chroma | Period trained | Total trained | Trained to position only | Trained to chroma | Average trained to chroma |
|---|---|---|---|---|---|---|
| | | *Hours* | *Per cent* | *Per cent* | *Per cent* | *Per cent* |
| Blue | Violet | 4 | [a] 80 | [a] 50 | 30 | 25 |
| | | 10¼ | 80 | 60 | 20 | |
| | | 11½ | 60 | 0 | 60 | |
| Do | Green | 2½ | 80 | 60 | 20 | 32 |
| | | 4 | 80 | 40 | 40 | |
| | | 6 | 70 | 50 | 20 | |
| | | 6 | 70 | 50 | 20 | |
| Green | Blue | 10½ | 100 | 60 | 40 | 40 |
| | | 7 | 90 | 50 | 40 | |
| Blue | Yellow | 8¼ | 100 | 87 | 13 | 16. |
| | | 9¾ | 90 | 70 | 20 | |
| Red | Blue | 8½ | 100 | 60 | 40 | 45 |
| | | 8½ | 80 | 30 | 50 | |
| Green | Red | 20 | 80 | 70 | 10 | 20 |
| | | 11½ | 80 | 50 | 30 | |
| | | 8¾ | 70 | 90 | −20 | |
| Red | Green | 12½ | 70 | 70 | 0 | 12. 5 |
| | | 8¾ | 70 | 40 | 30 | |
| | | 9 | 90 | 50 | 40 | |
| | | 30 | 80 | 80 | 0 | |
| Yellow | do | 40 | 90 | 80 | 10 | 17. 5 |
| | | 17 | 80 | 60 | 20 | |
| | | 8 | 90 | 50 | 40 | |

[a] In nearly all experiments the percentages given in these two columns are based on observation of the reactions of 10 bees. For instance, 80 per cent means that 8 of out 10 bees reacted as indicated

Of the three experiments tried in which selection did not occur, two were in the series in which the pair red versus green was used and one in the case of yellow versus green. These three experiments

gave a net percentage trained of minus 20, 0, and 0, respectively, minus 20 meaning, of course, that more bees went in the direction that led to food after the chromas were interchanged than went in that direction before. It seems, however, that no particular significance is to be attached to these values (which simply indicate complete lack of training to chroma) because the other experiments in the same series, performed on the next few succeeding days, gave higher values, from 10 to 40 per cent. It is probable, therefore, that these low values are merely accidental variations.

Do these results definitely establish the presence of chroma vision in honeybees? By definition, chroma vision is the ability to distinguish between diverse chromas of the same brilliance. There can be no question as to the ability of bees to distinguish between the chromas used in the experiments just described. (Table 5.) The only objection that can be raised is with reference to the values for stimulative effect of these chromas, found as described above and presented in Table 4. That is, if, perchance, owing to some fault in these tests, the relative brilliance of blue and violet, for example, were not really in the ratio of 40:4 (Table 4) but, say, 30:4, then their equalization on the basis of 40:4 would have left them really different in brilliance and the selection exhibited by the bees could have occurred on the basis of brilliance and not of chroma. But if it were true that the bees selected these chromas on the basis of brilliance alone, then, by varying in both directions the intensity of one member of any given pair of chromas, one ought to find somewhere an intensity at which its brilliance is just equal to that of the other chroma of the pair and produce thus a condition in which no selection would occur.

A series of experiments of this kind was performed, using the chromas yellow and green, which, according to Table 4, have a relative brilliance of 20:30. In the first experiments the chromas were equalized on this basis (lamps set 32.6 cm. from yellow filter, 40 cm. from green filter) and gave in four experiments percentages of bees trained to chroma of 0, 10, 20, and 40, having an average of 17.5. Then the intensity of the yellow was reduced to 75 per cent of its previous value (distance of lamp increased to 37.7 cm.), and two experiments gave percentages of 20 and 60, or an average of 40. Then the intensity of the yellow was still further reduced, to 44 per cent of its original intensity (distance of lamp increased to 49 cm.), and two experiments gave percentages of 40 and 50, or an average of 45. Finally, the intensity of the yellow was increased to 125 per cent of its original intensity (distance of lamp decreased to 29.2 cm.) and three experiments gave percentages of 15, 10, and 23, or an average of 16. Hence, even though one refuses to accept the chosen stimulative values, in terms of white light, of the chromas considered in Table 4 as accurate, and uses instead various other relative intensities, the result is the same, within the purpose of this research; the bees continue to distinguish between the chromas.

It is therefore maintained that the presence of chroma vision in bees is established.

### THE NUMBER OF CHROMAS DISTINGUISHABLE BY BEES

It is interesting to observe, in passing, some work that has been done on the number of different chromas bees can distinguish and the bearing of this work on the problem of the experiments recorded

in this paper. Von Frisch's (*6, 7*) experiments in training bees to come for food to various colored papers led him to conclude that they are able to distinguish only two chromas, the short-wave region comprising the blue and violet and the long-wave region comprising the green, yellow, and light red, and that they are chroma blind to blue-green and dark red. Kühn and Pohl (*24*), using a similar method, but with sections of the mercury-vapor spectrum instead of colored papers, concluded that there are four regions of the spectrum distinguishable by bees—the yellow and green region, the blue-green region, the blue and violet region, and the ultra-violet region. Kühn (*22*), supplementing the mercury-vapor spectrum with the continuous spectrum from a carbon arc, defines these regions more precisely as having for limits the wave lengths 650 to 510 mμ for the red, yellow, and green region, 500 to 480 mμ for the blue-green region, 480 to 400 mμ for the blue-violet region, and 400 to 313 mμ for the ultra-violet region.

On the basis of the experiments recorded in the preceding pages, the writer (*4*) in 1928 contended that bees are also able to distinguish blue from violet and green from light red. In Table 5 of the present paper, for example, blue is shown to be distinguished from violet by 25 per cent of the bees, and green from red by 20 per cent in one group of experiments and 12.5 per cent in another. But the width of the band of spectrum transmitted by the filters used, as shown in Figure 5, prevented him from giving the proof for such a contention, and therefore in writing the present paper no point was made of it. That is, the blue might have been distinguished by the bees from the violet because of the amount of blue-green transmitted by the blue screen, and the green may have been distinguished from the red because of the amount of blue-green transmitted by the green screen. If the contention is true, however, there are altogether six chromas which a bee can distinguish.

But subsequent to the appearance of the paper (*4*) cited in the preceding paragraph, and also subsequent to the writing of the first part of the present paper, there has come to the writer's attention a short article by Kühn and Fraenkel (*23*), in which they state that further work along the line pursued by Kühn (*22*) has shown that in the region comprising red, yellow, and green, and again in that comprising blue and violet, there are three nuances of color qualities distinguishable by bees. Hence the total number of chromas which it is claimed bees can distinguish now stands at eight.

One wonders if further research will not disclose still other chromas in the spectrum which are visible to the honeybee. By way of comparison it is interesting to note that for the human eye, according to Nutting (*32, p. 60–61*), there are "from about 130 to 180 distinctly different pure hues between the red and violet, while from violet back to red through the purples and magentas there are about 20 additional steps as determined by their complementaries in the green."

## CONCLUSION

In view of the findings of the research described under "Methods and results" in the present article, it is maintained that the presence of chroma vision in bees is established, and that the conclusion of Lubbock, Von Frisch, Kühn, and others is confirmed. The very fact of chroma vision connotes a diversity of chromas distinguishable by

bees, several of which have been reported by investigators, and it is presumable that the number of such distinct chromas will be augmented by further research.

## III. ABILITY OF THE HONEYBEE TO DISTINGUISH DIFFERENCES OF BRIGHTNESS

It seems self-evident that any animal that sees at all must have some ability to distinguish differences in brightness. Particularly ought this to be true for the honeybee, which, as is well known, reacts strongly to light. For this reason one is surprised to find in the literature records of experiments in which it is indicated that bees are entirely unable to distinguish any except relatively enormous differences in brightness. Von Frisch (*7, p. 105*), for example, after arranging in the manner of a checkerboard a series of pieces of paper colored various shades of gray, trained bees to come for food to a given one of these papers; then he rearranged the papers in different order and took the food away to see if the bees would seek out the same shade of gray as that on which the food had previously been placed. But they did not; they went to all the grays. Only when he used a very dark gray or a very light gray for training did the bees exhibit any evidence of ability to pick out the corresponding shade. He concluded, therefore, that bees possess a very poorly developed sense of brightness.

Von Hess (*18*), on the contrary, using a method in which training of the bees was not involved, concluded that they have practically as acute a sense of brightness as does man. In one experiment, for example, he confined bees in a cubical glass box on two opposite sides of which were placed tunnels containing lamps, one of which could be moved within its tunnel nearer to or farther from the box. Between the tunnel and the glass box on each side was placed a piece of white paper to serve as a diffusion screen. When the intensity of the light on the two paper screens was very unequal the bees crowded together toward the brighter, when equal they distributed themselves at random throughout the box. Von Hess observed that when the intensities on the two screens were changed from equality to a ratio of 1.00:0.86 they began to appear different in brightness to his own eyes, and that when the ratio was changed slightly to 1.00:0.83 the bees began to distribute themselves unequally in their container. Other experiments gave similar results, indicating that the bee is only slightly less acute than man in distinguishing differences in brightness.

Kühn (*20*), however, came to a conclusion agreeing with that of Von Frisch. He trained bees to come for food to a narrow trough illuminated by a streak of white light of a given intensity. Then, after they had become well trained, he removed the trough and threw on the table with the original streak of light another streak of different intensity which crossed the former diagonally, the two streaks together thus making a figure like the letter X. When the bees now came searching for food they alighted on the more intense of the two streaks, no matter which was the one used in their training. Kühn (*20, p. 118*) concludes, "Auf eine bestimmte Helligkeit sind die Bienen in diesen Versuchen nicht dressiert und auch nicht dressierbar."

The writer has had occasion to use both the method involving training and that involving merely untrained reactions. By use of the former method he (*4*) obtained evidence which led him to conclude that bees are "trainable" to differences in brightness. Using the same apparatus as that employed in testing chroma vision, described in Part II of this paper (fig. 9), but without the color filters, and the same method of procedure as described there, he was able to show that bees can distinguish two illuminated areas when one is as much as, or more than, 4 times as bright as the other, but probably not when one is only 1.3 times as bright as the other.

By use of a method involving only the untrained (instinctive) reactions of bees, the writer also demonstrated their ability to distinguish differences in brightness. The method used is described in the experiments dealt with in Part I of this paper. Bees were placed at one end of a dark box and allowed to walk toward two illuminated areas situated about 10 cm. apart at the opposite end of the box. In some experiments the illuminations of these areas were made equal in intensity and in others unequal in a variety of widely separated proportions. It was found, in brief (Table 2), that when the intensity of one was decreased (by large intervals) the relative number of bees going to that one decreased also, not in direct proportion but according to a curve (fig. 2) discussed there and of no particular interest here. That set of experiments did, however, establish a method of investigating this problem and confirmed Von Hess's conclusion to the extent that bees do instinctively distinguish between the brightness of two illuminated areas provided they are sufficiently different in brightness, but it did not show the *least* difference in brightness that bees can distinguish. (The ratio given in Table 2 which represents unequal intensities having the smallest difference in brightness is 0.50, which means, of course, that one intensity was half as great as the other.)

What is evidently needed, therefore, is a series of experiments to test in a quantitative way the bees' ability to distinguish differences in brightness.

Moreover, since at the present time there is much interest in comparisons of the acuity of various senses in bees with that of the corresponding senses in human beings, it also seems valuable to make another test of the relative acuity of the sense of brightness in these two. It was commonly believed in former times that the bee's senses are remarkably acute, but most of the results of actual tests have shown that they are less acute than those of man. As to taste, for example, Von Frisch (*9*) finds that the bee appears to be less acute than man for sweet and for bitter; and as to smell (*8*) it is said to be no more acute than man. In regard to sight, bees are far less able to distinguish chromas than we are, there being only eight chromas distinguishable by bees, according to Kühn and Fraenkel (*23*), in contrast to the 150 or so distinguishable by man; and in ability to distinguish details of shape and form they are far less acute than man (*2, 16*); according to Hecht (*15*) they are about one one-hundredth as acute. The question thus persists as to how bees compare with human beings in the ability to distinguish differences in brightness. Are they very much inferior to man, as Von Frisch and Kühn maintain, or practically equal to man, as Von Hess maintains? Although there is available much information on this subject in regard to human

beings, as for example that reported by Nutting (*32*), it can not, in fairness to the bees, be used in this comparison because it has been obtained with much more refined apparatus than can be used with bees.

A series of experiments was made, therefore, to obtain with the same apparatus for both bees and human beings as accurate quantitative measurements as possible of their ability to distinguish differences in brightness. These experiments are now to be described.

## METHOD

The apparatus (fig. 11) was essentially the same as that used in a previous series of experiments (Part I). It consisted of a shallow, rectangular box, *a*, covered with wire screen, 67 by 26 by 4 cm. inside, and of three boxes, *b*, *c*, and *d*, for holding lamps. The smallest lamp box, *b*, was placed at one end, designated as the left-hand end, of the large box *a*, the two others at the opposite or right-hand end. Light from the lamp in box *b* illuminated a small area of a ground-glass screen *e* placed in the center of the left-hand end of the large box *a*, and the lamps in boxes *c* and *d* illuminated areas 6.5 by 13 mm. on the

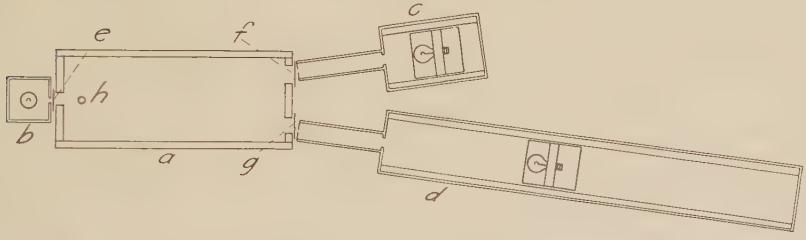


FIGURE 11.—Diagram of apparatus used in studying the ability of bees and of human beings to distinguish between small differences of brightness. See text for explanation

ground-glass screens *f* and *g*, placed equidistant from the corners at the right-hand end of the large box *a*. A hole in the floor of the large box in the mid-line near the left-hand end permitted the entrance of bees. The whole apparatus was placed in a dark room. Box *b* contained a 15-watt lamp, the boxes *c* and *d* either 10-watt or 75-watt lamps, always both the same in any one test. The lamp in box *c* remained always at the constant distance of 40 cm. from the screen *f*; the lamp in box *d* was placed either at 40 cm. from screen *g*, where the intensity on the screen was equal to that produced by the lamp in box *c*, or at 42.1 cm., 44.7 cm., 48.0 cm., 51.6 cm., 56.0 cm., 63.2 cm., or 73.0 cm., where the intensity was reduced, respectively, to 0.9, 0.8, 0.7, 0.6, 0.5, 0.4, or 0.3 the value of that produced by the lamp in box *c*. The lamps in boxes *c* and *d* were interchanged at the middle of every experiment to neutralize any possible difference in brightness between the two lamps. The lengths of the wires leading from the switch to the lamp sockets in *c* and *d* were made equal, in order to obviate any difference in brightness due to differences in resistance.

In performing an experiment with this apparatus, a bee was captured at a feeder,[14] in a small screen-wire cylinder about the size of an ordi-

[14] Field bees must be used. Hive bees that have not yet begun to collect from the field are not positive to light.

nary test tube, taken inside the dark room, and fed with sugar water (by inverting over the screen-wire cylinder a small vial containing this liquid, its mouth covered with a layer of cheesecloth) until it was satiated,[15] then it was released into the large box *a* through the hole *h* in the floor. At the same time the lamps in boxes *c* and *d* were turned on, so that the bee on entering found itself confronted by two illuminated areas 60 cm. away and 10½ cm. apart. Sufficient light diffused from the illuminated areas to enable the observer to see the bee in the box. The bee now walked toward the spots of light, soon veering toward one or the other, and eventually bumping into one of them if allowed to proceed far enough. Ordinarily, however, as soon as it could be ascertained which lighted area the bee was headed for, the lamps in boxes *c* and *d* were turned off and that in box *b* turned on, and the bee immediately turned around and walked toward the source of light in the latter box. When it had come near the hole in the floor through which it had entered, the lamp in *b* was suddenly turned off and the lamps in *c* and *d* turned on, whereupon the bee turned around and walked again toward the right-hand end of the box, going toward one or the other of the areas illuminated by the lamps in *c* and *d*.

This marching and countermarching was continued until, for most of the tests, the bee had made five trips toward the right-hand end of the box. Detailed records were kept as to which area it went on each trip. Such a record, giving the responses of 20 bees to areas whose intensities of illumination had the ratio of 0.3 : 1.0, is presented in Table 6. In the summarized results records were made (1) of the total responses of all bees to each pair of illuminations and (2) of the sum of the initial responses of individual bees to a pair of illuminations. It was thought that the initial response of the bee when first faced with these two illuminated areas might better indicate which area really appeared the brighter to the bee than the sum of five reactions, but this idea does not appear to be correct.

After one bee had made five successive trips it was taken out into the open and released and another bee captured and given the same treatment. Experience had previously shown that after five such trips many bees become sluggish, and begin to wander aimlessly about the box, apparently having lost much of their positiveness to light.

For most of the tests a total of 30 bees were used for each pair of illuminations, giving therefore 150 responses. For some pairs of illuminations data previously gathered were included, giving as many as 1,150 responses for a single pair. Eight pairs of illuminations were employed, the ratios of intensities of which have been given, with two sizes of lamps, making 16 tests in all.

[15] The feeding tends to quiet the bees and prevent them from racing wildly over the box when released into it.

TABLE 6.—*Detailed record of two tests, giving reactions of bees to a pair of illuminations having intensities in the ratio 0.3:1.0* [a]

[Left-hand lamp 10-watt, at a distance of 40 cm.; right-hand lamp 10-watt, at a distance of 73 cm.]

| Date August, 1928 | Hour | Bee No. | Reactions | Date August, 1928 | Hour | Bee No. | Reactions |
|---|---|---|---|---|---|---|---|
| 7 | 10.30 | 1851 | | 7 | 3.35 | 1871 | |
| 7 | 10.40 | 1852 | | 7 | 3.40 | 1872 | |
| 7 | 10.45 | 1853 | | 7 | 3.45 | 1873 | |
| 7 | 10.50 | 1854 | | 7 | 3.50 | 1874 | |
| 7 | 11.00 | 1855 | | 8 | 9.30 | 1875 | |
| 7 | 11.05 | 1856 | | 8 | 9.35 | 1876 | |
| 7 | 11.10 | 1857 | | 8 | 9.40 | 1877 | |
| 7 | 11.15 | 1858 | | 8 | 9.45 | 1878 | |
| 7 | 11.35 | 1859 | | 8 | 9.50 | 1879 | |
| 7 | 11.45 | 1860 | | 8 | 9.55 | 1880 | |
| | | | 24 \| 26 | | | | 38 \| 12 |

[a] This table is an attempt to reproduce as exactly as is practicable in print a small part of the writer's record of the observations described in the text. Each bee used was assigned a number, to the right of which a series of five dots, reading downward, represents the five consecutive reactions of the bee. A dot to the left of the vertical line records the approach of the bee to the ground glass *f* (fig. 11), and one to the right of that line an approach to the ground glass *g*. The hours indicated in this table range from 9.30 a. m. to 3.50 p. m.

For comparison of the acuity of vision of the bee with that of man it is evident that the same or similar apparatus must be used. The abundant data already available for the perception by man of differences of brightness, such as that published by Nutting (*32*) in 1920, obtained with refined apparatus much of which can not be used for bees, would necessarily give man an unfair advantage in the comparison. In these experiments, therefore, human subjects were tested with the same apparatus as was used for bees.

The subjects were brought into the dark room one at a time and placed in such a position that they faced toward the two screens *f* and *g*. After allowing from one to two minutes for adaptation of the eyes to the darkness (corresponding to the time allowed for the bees to feed), the lamps in boxes *c* and *d* were turned on and the subject was asked which spot of light appeared the more brilliant to him. After he had answered, others (a total of from 1 to 11 in different tests) were brought in and tested similarly. Then the relative intensity of illumination by the two lamps was changed and the same or other subjects tested again. Seventy-five-watt lamps were used in all tests, set to illuminate the ground-glass screens at intensities in the ratios 1.0 : 1.0, 0.9 : 1.0, 0.8 : 1.0, and 0.7 : 1.0. The positions of boxes *c* and *d* were interchanged frequently, and every known precaution was taken to avoid giving the subjects any clues as to which area really was the brighter. Most of the subjects did not even know how the apparatus was constructed until after the tests were completed.

## RESULTS

The results for bees are presented in Table 7, and those for human subjects in Table 8. Figures 12 and 13 present graphically the results for bees, the former with illumination by 10-watt lamps, and the latter with illumination by 75-watt lamps. It will be seen that when the illuminations of the two areas were the same the number of responses to each, for both bees and human beings, was the same with the exception of the 30 initial responses recorded for bees when the 10-watt lamps were used. (Fig. 12.) That this exception is due to the small number of bees employed is indicated by the fact that the observation of 1,150 and 1,000 responses, respectively, in the other two experiments with intensity ratio of 1.0:1.0 gave results almost exactly 1.0:1.0. (Table 7.) When the intensity of illumination for the one area was lowered to 0.9 (Table 7, intensity ratio 0.9:1.0) the response of bees to the dimmer illumination also decreased in most experiments, but when the intensity was further lowered to 0.8, the response of bees to the dimmer in all experiments increased again until more than half were going to the dimmer area. (Table 7 and Figures 12 and 13.) This indicates that bees do not distinguish between illuminated areas under these conditions even when the intensity of one illumination is reduced to 80 per cent of the intensity of the other. When it was reduced to 0.7, however, in most experiments the dimmer area attracted fewer bees than the brighter, and when reduced to 0.6, 0.5, 0.4, and 0.3 it attracted on the whole fewer and fewer bees, although the decrease in response of the bees was not directly proportional to the decrease in intensity of the variable illumination.

TABLE 7.—*Summary of experiments to test the ability of bees to distinguish between the intensity of illumination of two illuminated areas, with results for each ratio of intensities used*

AREAS ILLUMINATED BY 10-WATT LAMPS [a]

| Variable illumination in terms of constant illumination | Bees used in observing total responses | Total responses observed | Total responses to variable illumination, in terms of total responses to constant illumination | Bees used in observing initial responses | Initial responses to variable illumination, in terms of initial responses to constant illumination |
|---|---|---|---|---|---|
| *Ratio* | *Number* | *Number* | *Ratio* | *Number* | *Ratio* |
| 1.0 | 100 | 1,150 | 1.003 | 30 | 1.31 |
| .9 | 30 | 150 | .90 | 30 | .67 |
| .8 | 30 | 150 | 1.11 | 30 | 1.14 |
| .7 | 30 | 200 | 1.06 | 30 | .67 |
| .6 | 30 | 150 | .67 | 30 | .88 |
| .5 | 100 | 900 | .77 | 40 | .29 |
| .4 | 30 | 150 | .79 | 30 | .76 |
| .3 | 30 | 150 | .61 | 30 | .36 |

AREAS ILLUMINATED BY 75-WATT LAMPS [a]

| | | | | | |
|---|---|---|---|---|---|
| 1.0 | 60 | 1,000 | 1.008 | | |
| .9 | 30 | 150 | .92 | 30 | 1.14 |
| .8 | 30 | 150 | 1.03 | 30 | 1.50 |
| .7 | 30 | 150 | .76 | 30 | .67 |
| .6 | 30 | 150 | .60 | 30 | .43 |
| .5 | 30 | 150 | .61 | 30 | .50 |
| .4 | 30 | 150 | .52 | 30 | .20 |
| .3 | 30 | 150 | .50 | 30 | .67 |

[a] For the 10-watt lamp at the distance of 40 cm., the minimum distance used, the intensity of illumination on the screen was approximately 45 meter candles; for a 75-watt lamp at the same distance, approximately 580 meter candles.

TABLE 8.—*Summary of results of experiments to test the ability of human beings to distinguish between the intensities of illumination of two illuminated areas,* [a] *with results for each ratio of intensities used*

| Variable illumination in terms of constant illumination | Subjects used | Correct choices | Incorrect choices | Total choices | Correct choices in terms of total choices |
|---|---|---|---|---|---|
| *Ratio* | *Number* | *Number* | *Number* | *Number* | *Per cent* |
| 1.0 | 2 | 2 | 0 | 2 | 100.0 |
| .9 | 12 | 15 | 9 | 24 | 62.5 |
| .8 | 9 | 11 | 2 | 13 | 84.6 |
| .7 | 8 | 8 | 0 | 8 | 100.0 |

[a] Areas illuminated by 75-watt lamps. At the distance of 40 cm. the intensity of illumination was approximately 580 meter candles.

It will be observed in Figures 12 and 13 that for total responses the results are clearer and more consistent (the curves smoother) with the use of the 75-watt lamp than with the 10-watt lamp. For initial responses neither lamp seemed to have any advantage. In comparing total responses with initial responses, however, the total responses give much more consistent results.

It may be concluded, therefore, that under the conditions of intensity, type of apparatus, and adaptation to darkness used here bees

begin to distinguish between two illuminated areas when the difference between their intensities of illumination is increased to that represented by the ratio 0.7:1.0, but do not distinguish between them if the difference is equal to or less than that represented by the ratio 0.8:1.0.

When these results are compared with results obtained with human subjects the difference is striking. When the areas were made equal in brightness the human subjects used could see no difference between them (Table 8), as was to be expected. When the brightness of one area was reduced to 0.9 of that of the other, however, 15 out of 24 subjects, or 62.5 per cent, selected it as the dimmer. When further reduced to 0.8, in 11 out of 13 tests, or 84.6 per cent, that area was

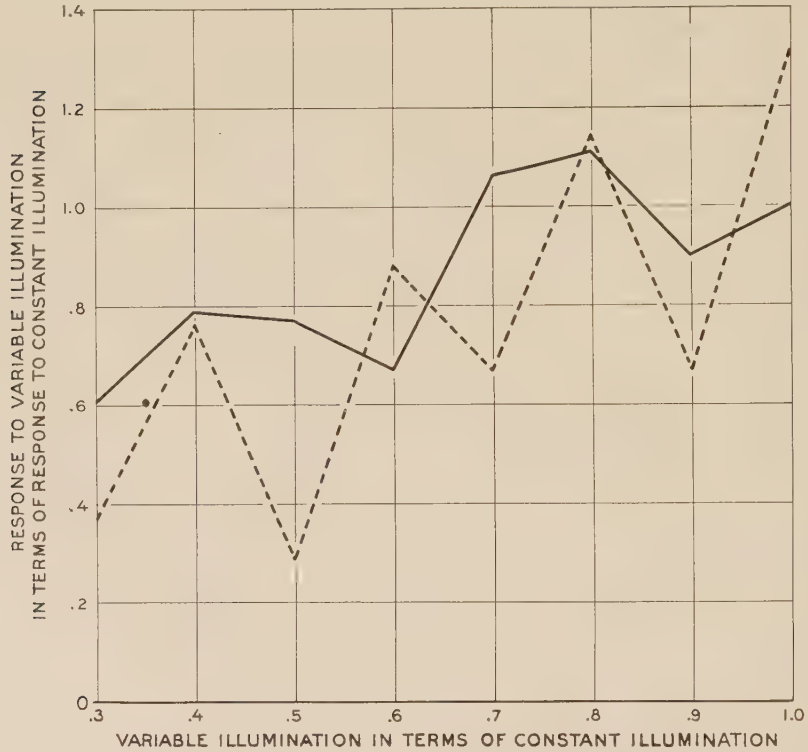


FIGURE 12.—Relative response of bees to illuminations of various relative intensities, when 10-watt lamps were used as sources of illumination. Broken line, averages of initial responses of bees; solid line, averages of total responses

selected as the dimmer, and when reduced to 0.7, all of the eight subjects selected it as the dimmer.

It may be concluded, therefore, that under the conditions of intensity, type of apparatus, and adaptation to darkness prevailing here, human beings can usually distinguish between two illuminated areas when the difference is only that represented by the ratio 0.9:1.0 and can unmistakably distinguish between them when the difference is as much as that represented by the ratio 0.7:1.0; and, accordingly, that human beings are considerably more sensitive than bees to differences in intensity of illumination.

Such a qualitative statement as the above seems amply justified by these experiments, but to state quantitatively how much more sensitive men are than bees requires a great deal of caution, as indeed does the quantitative comparison of the behavior of man with that of any other animal. Caution is necessary here first of all because of a difference in the nature of the response; the human subjects were asked to state which of the two areas appeared brighter (or dimmer) to them, whereas one obtained similar information from the bees by observing their movements. With human subjects the response is simple,

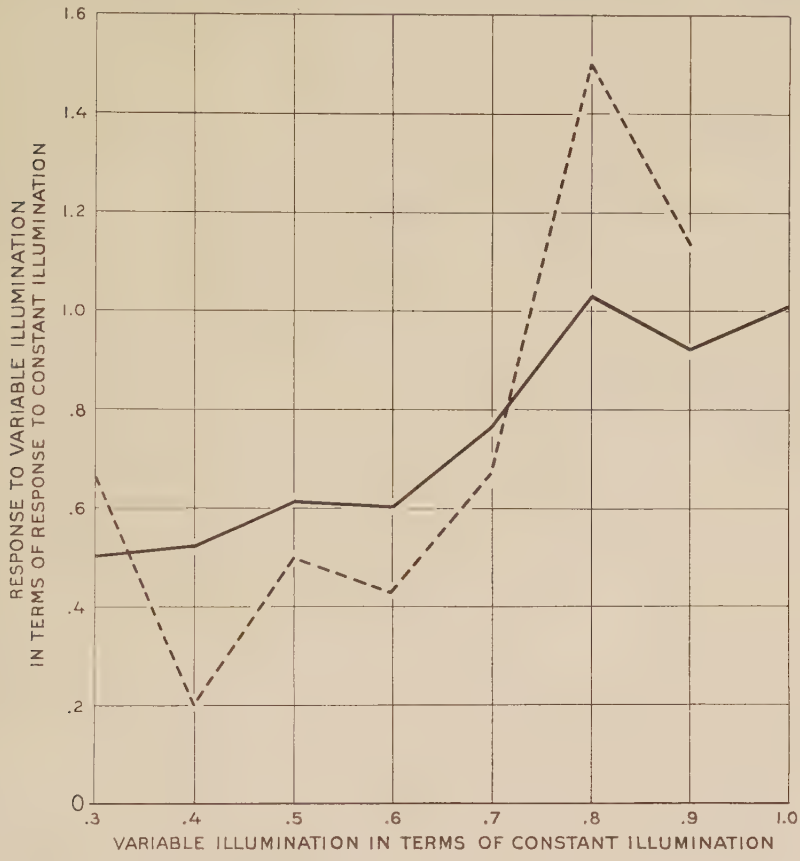


FIGURE 13.—Relative response of bees to illuminations of various relative intensities, when 75-watt lamps were used as sources of illumination. Broken line, averages of initial responses of bees; solid line, averages of total responses

involving only sight and speech in a reaction hardly more than a simple reflex. With bees the response may be enormously complex, since the reaction is in all probability an attempt to escape from the box, which is influenced on occasion by a difference in the intensities of two separate illuminations, and is consequently a very complicated reflex, conditioned not only by the metabolic condition of the bee but by all its past experiences in dealing with such situations.

Caution is necessary, secondly, because of a fact which may be closely correlated with the first; namely, a wide variation in the re-

actions of the bees under identical conditions. One of the most striking examples of this was a test in which reactions were obtained of 10 bees to two intensities whose ratio was 0.3 : 1.0 (with 10-watt lamps); of the first 50 reactions obtained 24 were toward the intensity of 1.0, while 26 were toward the intensity of 0.3, whereas of the last 50 reactions obtained with 10 other bees, 38 were toward the intensity of 1.0 and 12 toward the intensity of 0.3. If one had stopped with the first 50 reactions it would have appeared that the bees did not distinguish between intensities so widely different as 1.0 and 0.3. The detailed record of these two tests is given in Table 6. Until one can control more factors influencing the reactions of bees in such experiments as these, one must simply use such large numbers that variations will tend to fall equally on each side of the correct value.

Although a definite quantitative comparison of acuity in bees and in human beings in distinguishing differences of brightness is thus not permissible from the results of these experiments, it is clear that human beings are considerably more acute in this respect than bees, and the method here followed offers the possibility of comparing other insects with bees, provided large numbers of each insect are used.

### CONCLUSION

From the results of these experiments it appears that neither the conclusion of Von Frisch and Kühn that bees distinguish only enormous differences in brightness, nor that of Von Hess that bees are practically as acute as man in this ability is correct. The more nearly correct conclusion seems to be in the nature of a compromise between the two, namely, that bees begin to distinguish between two illuminated areas when the intensity of one is reduced to at least 70 per cent of the intensity of the other, whereas human beings distinguish between them equally well when the intensity of the one is reduced to only 90 per cent of that of the other.

## GENERAL CONCLUSIONS

The upper limit of the spectrum for the honeybee extends to at least wave length 677 mμ in the red. The difference between this result and that of 650 mμ found by Kühn is probably due to a difference in the intensity of the spectral light used in the two sets of experiments. The lower limit was not ascertained in the research here reported, but according to Kühn it extends to at least 313 mμ.

The point of maximum stimulative efficiency for the honeybee is in the yellow-green at about 553mμ, which corresponds rather closely with that for man. From this point the efficiency decreases more rapidly for bees than for man toward the longer wave lengths, but more slowly than for man toward the shorter wave lengths, being at 431 mμ still fully 10 per cent of the maximum.

Untrained bees, when allowed to walk toward two sources of light of the same quality, placed near together at the end of a rectangular box, go to the brighter more often than to the fainter, but not in direct proportion to the relative brightness of the two. The curve representing the relation between relative brightness and relative magnitude of response is a polynomial one, of such form that the curve showing the relation between the logarithms of the two related variables is an approximately straight line.

The presence of chroma vision in bees, already strongly indicated by the work of previous investigators, is more clearly established.

For the moderate intensities used in these experiments (Part III), the bee begins to distinguish between two illuminated areas when the illumination of one is reduced to an intensity 70 per cent as great as that of the other. The ability to distinguish is slightly less pronounced when the intensity of illumination is low (45 meter candles on the brighter area) than when it is high (580 meter candles on the brighter area).

Human beings, tested with the same apparatus as that used for bees (using the higher intensity of illumination), begin to distinguish between the brightness of two illuminated areas when the intensity of one is reduced to 90 per cent of that of the other; this distinction is fairly accurate when the intensity of the one is reduced to 80 per cent, and is quite accurate when the reduction reaches 70 per cent. Human beings are, therefore, considerably more acute than bees in ability to distinguish differences in brightness.

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## VITA

Lloyd Millard Bertholf was born in Sedgwick Co., Kansas, December 15, 1899. He attended the public schools of Kansas, being graduated from the High School at Spivey in 1917. The next two school years were spend at Friends University, Wichita, Kansas, (except for the first semester of 1918-19, when in army service) and the next year and a half at Southwestern College, Winfield, Kansas. In the middle of his senior year at the latter college he had an opportunity to accept an assistantship at the Johns Hopkins University, Department of Zoology, and came to the University at that time, receiving the degree of Bachelor of Arts *in absentia* from Southwestern College in June 1921. During the year 1921-22 he continued at the University, was away during the next two years serving as instructor in the North Carolina College for Women, Greensboro, N. C., but spent the next year (1924-25) again at the University. During this year he was also in charge of the Department of Biology at Western Maryland College, as Professor of Biology. He was awarded the degree of Master of Arts by the University in June 1925. The next two years were spent in teaching at Western Maryland College. He returned again to the University for the year 1927-28 as Bruce fellow, and completed the requirements for the degree of Doctor of Philosophy. The six summers from 1922 to 1927 inclusive were spent in investigations at the Bee Culture Laboratory of the U. S. Department of Agriculture, Washington, D. C.